December 1955

VOL. 67, No. 4 PAGES 233-328

The Wilson Bulletin

Published by

The Wilson Ornithological Society

at

Lawrence, Kansas

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Founded December 3, 1888

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THE WILSON BULLETIN

The official organ of The Wilson Ornithological Society, published quarterly, in March, June, September, and December, at Lawrence, Kansas. In the United States the subscription price is $3.00 a year, effective in 1951. Single copies, 75 cents. Outside of the United States the rate is $3.25. Single copies, 85 cents. Subscriptions, changes of address and claims for undelivered copies should be sent to the Treasurer. Most back issues of the *Bulletin* are available (at 50 cents each for 1950 and earlier years, 75 cents each for 1951 and subsequent years) and may be ordered from the Treasurer.

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Entered as second class matter at Lawrence, Kansas. Additional entry at Ann Arbor, Mich.

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by The Wilson Ornithological Society

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THE BREEDING CYCLE IN THE BANK SWALLOW

BY ARNOLD J. PETERSEN

THE BEHAVIOR of birds during a considerable part of the year is dominated by activities directly related to reproduction. It is not strange that such striking sequences of behavior recurring annually in the lives of birds have long held the interest of man. Only recently, however, have refined techniques of observation been developed which can be applied to field studies of natural behavior.

A general relationship has long been recognized between morphological changes in the reproductive organs and the orderly progress of the breeding cycle in birds. General summaries of these relationships together with interpretations of their endocrinological mechanisms have been provided by Marshall (1929), Huxley (1932), and Groebbels (1937). More detailed work on gonadal recrudescence in relation to breeding activity has been reported for various species by Blanchard (1941), Höhn (1947), Marshall (1951, 1952*a*,*b*,*c*) and others, and many workers have investigated the development of the reproductive structures in relation to environmental factors (Burger, 1949; Farner, 1950). Extensions of these descriptive studies to include various aspects of blood chemistry have been made for domestic pigeons and doves by Riddle and his associates (Riddle, 1937*a*; Schooley, 1937; and Riddle, 1942). Experimental investigations of the relationships between breeding behavior and physiology have been reviewed by Bullough (1945), Beach (1948), and Collias (1950).

The purpose of this study is to examine certain aspects of the behavioral and physiological cycles of a wild species for correlations that might shed light on the physiological regulation of natural breeding behavior. This study was carried out in the vicinity of Madison, Wisconsin, during the years 1950 through 1953 and was submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Wisconsin.

ACKNOWLEDGMENTS

This work was carried on under the guidance of Dr. John T. Emlen to whom I am indebted for assistance in planning and practical help and encouragement throughout the study. A research assistantship from the Wisconsin Alumni Research Foundation and a grant from the Louis Agassiz Fuertes Research Fund of the Wilson Ornithological Club are gratefully acknowledged.

I wish to thank the following individuals for many kinds of help: Dr. R. K. Meyer for suggestions regarding the laboratory work, Dr. Nellie M. Bilstad for advice in the histological study, Charles M. Kagawa and Dr. W. H.

McShan for assistance in chemical techniques, Prof. H. H. Hull of Wisconsin Soils Testing Laboratory for assistance with soil analyses, L. A. Joos of the U.S. Weather Bureau for climatological data, and many of my colleagues at the University of Wisconsin who assisted on collecting trips.

The Bank Swallow as a Subject for Study

The Bank Swallow (*Riparia riparia*) was selected as the subject for this study of breeding cycles for several reasons. The species breeds in easily located colonies of up to several hundred pairs and is common in the vicinity of Madison. The nests are built in burrows which are usually readily accessible and from which the birds can easily be collected. Behavioral characteristics of special interest include a sharing of many of the breeding activities of the two sexes, a long period of nestling development, and a fairly close synchrony of activities within a colony.

Difficulties were presented by the closed nature of the nests, screening many of the breeding activities from view. The similarity of the sexes in appearance and behavior and the concentrations of many pairs in a closely-nesting colony made individual recognition difficult. Finally, the small size of the species placed severe restrictions on the chemical studies and necessitated special techniques.

Previous studies of Bank Swallow behavior provided a background of information helpful in the planning and interpretation of my work. The most extensive of these are Stoner's observations of colony composition and Beyer's (1938) observations of activity within the nest chamber from a darkened pit dug behind the burrow. A number of observations reported for the species in England, where it is called the Sand Martin, are noted below. In none of these were techniques for recognition of individual birds used and sex was known only by dissection.

I. Behavior Cycle of the Bank Swallow

Procedures in Behavior Observations

As many colonies of Bank Swallows as possible were located in Dane County, Wisconsin. Specimens for morphological and physiological studies were collected at certain of the colonies; other colonies were left undisturbed for behavior studies. Collection and autopsy procedures will be described beyond.

Observations of the behavior cycle were made principally at a colony on Nine Springs Creek, two miles south of Madison. The creek is a temporary stream which has eroded a bank in a pastured meadow on the Alfred Keller farm. An observation blind protected by an electric fence from trampling by cows was placed 15 feet from the bank, affording a clear view of nearly

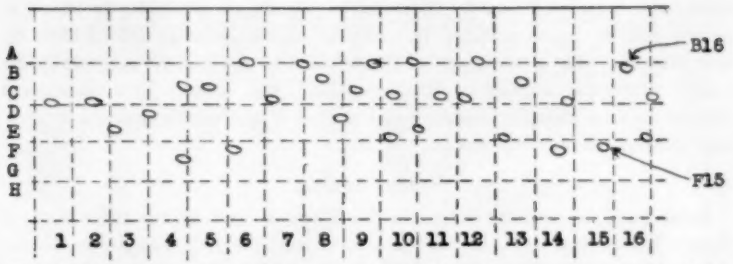

FIG. 1. Map of Bank Swallow burrow entrances illustrating the method of identifying burrows.

all of the burrow entrances. The bank was only six feet high, so the burrows were easily accessible for observation of their interiors and for trapping of the occupants. I attempted to keep the disturbance of my activities at the necessary minimum, and there was no other human interference at this colony.

Individual burrows were identified and designated on a scale map of the burrow entrances with the help of a grid overlay, giving each burrow a letter and a number identification (Fig. 1). Mimeographed copies of this colony map were used for recording observations.

Birds were captured for marking by a method described by Morris (1942). Transparent plastic bags (quart-size frozen food bags) were held by a rubber band over one end of a roll of cardboard and the other end of the cardboard fitted into the burrow entrance. These traps were usually placed just before dawn but were also used with success at various times of day.

The captured birds were individually marked by painting the outer one-inch of the outer or ninth primary feather with airplane dope. The tips of the seventh and eighth primaries were clipped off to completely expose the color marks. Thus, each bird was given a combination of two colors which became its name (for example: left wing-tip orange, right wing-tip red, was abbreviated *OR*).

Sex was determined by presence of a brood patch in females and absence of a brood patch in males.

Eleven broods of nestlings were given colored leg bands (numbered Fish and Wildlife Service bands dipped in airplane dope) designating their brood. This marking proved useful for observations of these birds in the late nesting and early post-nesting stages.

On-the-spot notes were made of activity observed at the colony with the time, and whenever possible specific birds and locations of each action

recorded. At times it was found useful to prepare simple tables in which to record activity more quickly. In order to obtain accurate information on nest contents with a minimum of disturbance to the colony a specially designed periscope, dubbed a "Ripariascope," was made. This instrument lighted the nest chamber enabling one to view a nest and it contents quickly and without alteration of the burrow.

Spring Arrival

Bank Swallows usually arrive in the Madison area in the latter part of April. The arrival dates in the years 1947 through 1952 (according to the observations in the University of Wisconsin Zoology Department and Kumlien Club files) range from April 19th to 26th, the average date for the six years being April 22. Each of these observations was made by an experienced ornithologist, so it may be considered a positive record of presence of the species on that date. However, it is entirely possible that in some years the species may have been present for one or several days before the first observations recorded in this file. On the other hand such an observation may indicate the arrival of only a very few erratic individuals. Nevertheless, since these are the best available records of Bank Swallow arrival, it would seem worthwhile to consider their relation to climatological factors.

The April daily mean temperatures and dates of arrival for these years are shown in Figure 2 and summarized in Table 1. These data indicate that Bank Swallows will arrive in Madison earlier than the average date of April 22 when the mean temperatures of the preceding 15 days have averaged above normal. Arrival will be delayed beyond April 22 if the 15

Table 1

Arrival of Bank Swallows at Madison, Wisconsin

Year (In order of arrival dates)	Date of arrival	Mean Temperatures, °F			
		On date of arrival		Preceding 15 days	
		Temp.	Departure from normal	Temp.	Departure from normal
*1919	April 13	50	+ 6	44.1	+3.3
1948	April 19	69	+21	48.0	+4.5
1952	" 20	63	+15	44.1	+0.1
1949	" 22	58	+10	44.3	−0.7
1947	" 22	46	− 2	41.1	−3.8
1950	" 23	49	0	40.4	−4.8
1951	" 26	46	− 4	40.7	−6.0
Averages.....	April 22	55	+ 6.6	43.1	−1.8

*Not included in average.

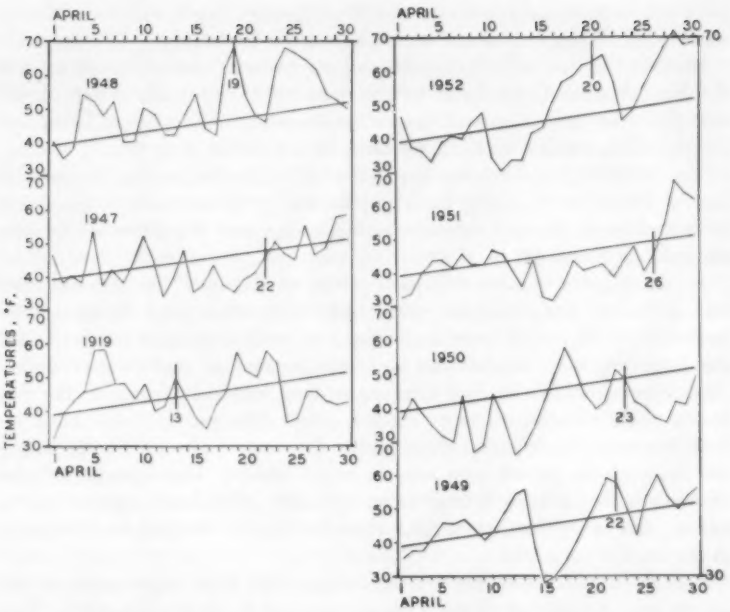

FIG. 2. Spring migration and temperature. Smooth diagonal line represents normal temperature; jagged line connects mean daily temperatures. Vertical bar indicates date of arrival of Bank Swallows at Madison.

days preceding arrival are considerably below normal for the period.

Taylor's observation (Schorger, 1931) of Bank Swallows on April 13, 1919, is the earliest known arrival date for Dane County. Since the temperature on that date was only six degrees above normal and the preceding 15 days averaged only 3.3 degrees above normal, it would seem that this was probably a record of a few birds advancing beyond the usual conditions for migration of the species, about a week ahead of the true migration front. Further evidence to this supposition is the fact that Taylor (unpublished field notes) did not find other late-arriving species of Hirundinidae unusually early in 1919.

Arrival of Bank Swallows at the breeding site may not be coincident with arrival in the area, particularly if the weather is cloudy and cold. In 1950 the species was observed at Madison on April 23. The next nine days were cloudy with mean temperatures below normal and, although there were additional reports of Bank Swallows in the area during this time, the birds

were not seen in daily visits to the Nine Springs Creek site until May 3, when warm temperatures and clear skies again prevailed.

In 1951, on the other hand, the earliest arrivals were six birds seen at the Nine Springs Creek bank on the morning of April 26, a day of full sunlight. The following week was a succession of warm bright days, and an increasing number of birds was seen at the colony each day.

Nice (1937) found in her Song Sparrows that the timing of each of several activities, the taking up of territories by resident males, the spring arrival of migrants, and the start of egg-laying, was dependent on its own temperature threshold.

In unfavorable weather the early visits to the sand banks were brief and sporadic. Early arrivals were more likely to be seen foraging over bodies of water, which seem to be the best feeding grounds in April. On the first bright warm day the birds congregated at traditional breeding sites, entering old holes and clinging to any ledges or irregularities that lent support. Flights in large circles within 100 yards of the bank by individuals or small loose groups were frequent, but such flights lacked the close intense pursuit seen later in sexual chases. That interest in holes and ledges on the bank seemed to be by single individuals and that sexual chases were not observed suggest that few if any of these early visitors at the bank were paired.

Positive social forces are strong during these first appearances at the colony site. Usually all of the birds are engaged in the same activity. That is, all are circling overhead, or all are occupied on the bank. Alarm calls frequently put the entire group to flight.

Pair Formation

On successive favorable days the numbers of birds visiting the breeding site and the time they spend there increase. Gradually the increasing number of sexual flights and association of certain *pairs* of birds with particular burrows or areas of the bank suggest that more and more of these birds are paired.

Most Bank Swallows secure mates very quickly during early visits to the colony site. In other instances a week or more may elapse before a pair is formed. Observations of such cases reveal the following sequence of events in pair formation: An unpaired bird (a male in one instance where sex was subsequently determined) selects a burrow site. In the case of some early arrivals this may be a burrow of the previous year. Later the site is more commonly any suitable part of the bank on which the bird can maintain a foothold.

Having selected a site, or territory, a bird defends it against intrusion by use of vocal threats and physical force. Such vocal threat or "territorial

song" is a loud coarse twittering, broken into long irregular phrases and directed with apparent vehemence with outstretched neck and bill pointed toward the intruder. These sputterings may be continued for a minute or more, and usually have the result of driving the intruder away. While territorial song seems to me to be aggressive in nature, certain observations suggest that it may serve to attract unmated birds. During this period when territories are being established, it is common to see groups of several or a dozen or more birds move along the bank in hovering flight, and again such birds will hover at a defended niche or even alight and cling to the bank. They are usually quickly driven off by the resident defenders, only to circle and return to the same or another defended ledge.

Against persistent intruders who perch very close, the defending bird intersperses his sputterings with forceful pushes with the bill. Still more forcibly a bird may fly from his ledge or burrow, turn, and, hovering over the intruder, grasp his neck feathers in his bill and thus pull him from the bank. Frequently two such birds become locked in combat and fall together from the bank, sometimes continuing their struggles for many seconds on the ground below.

One among those which continue to return to a defended spot is eventually tolerated and becomes recognized by the bird holding the territory as his mate. Sexual recognition probably depends on a female sexual characteristic of greater persistence in returning to a site in the face of apparent aggressive threat and attack.

One marked male defended his partially-completed burrow with great vigor following disappearance of his first mate. Later, having accepted a new mate, he was noticeably more tolerant of nearby birds whenever the mate was present in the burrow, than when she was away.

Birds entering burrows other than their own usually showed a certain hesitancy of manner contrasting with the deliberate actions of a bird entering its own burrow. Once a pair is formed both members of the pair share in territorial defense, both vocally and physically.

Maintenance of the Pairing Bond

Joint participation of paired birds in breeding activities, such as territorial defense and, as will be described later, burrow digging, nest building, incubation, and care of young, probably contributes to the strength of the attachment. Other activities which appear to serve more specifically toward maintenance of the pairing bond are sexual chase, mating song, and copulation.

Sexual chase is a prominent feature of the behavior of mated birds from the time of pair formation until incubation begins and it is continued (but much less frequently) into the incubation period. In sexual chase the

female followed closely by her mate flies from the burrow and after either brief or extensive circling flight usually returns to the burrow. The male maintains close pursuit throughout whatever intricate maneuvers the female makes, and he sings continuously. I have observed sexual chase 10 or 15 times in marked pairs in which the sexes were known and found that in every case the female flew ahead of the male. In a few chases where the birds flew close enough, I noted, as Tooby (1947) frequently observed in the Sand Martin, that it is only the pursuer, that is, the male, that sings.

This song differs from territorial song and from mating song in its being given exclusively by the male. Further, it is neither as loud and harsh as territorial song nor as soft and murmuring as the mating song. During the burrow digging stage it was often noted that sexual chase occurred immediately upon the return of one member of the pair after a brief absence from the burrow. On two occasions a male sitting beside his mate near the burrow entrance was seen to nudge her gently in the side with his bill until she flew, seemingly upon his invitation. In each instance the male followed her in sexual chase.

While sexual chase is clearly an activity of mated birds, a pair will very commonly be joined by one or more additional birds. Unmated birds have been observed to leave their defended niches and join in the sexual chase of pairs from nearby burrows.

The *mating song* is such an inconspicuous form of courtship behavior that it is likely to pass unnoticed amid the more striking hubbub of territorial disputes and sexual chase. Its occurrence is probably more general than my two recorded observations would suggest, although it is mentioned in no previous studies of Bank Swallows.

The mating song is a very soft, pleasing twittering by both members of a pair simultaneously while sitting quietly side by side or facing each other in the burrow opening. It is much more subdued than territorial song or even that of the male in sexual chase, so that it can be heard for only a short distance. (My observations were from a blind 20 feet from the burrows.) It can not be heard at all if nearby birds are engaged in territorial song. Mating song is a continuous succession of notes, not broken into phrases like territorial song. In both cases observed the pairs were in the egg-laying phase and it may be an adjunct of copulatory behavior, commonly occurring as I believe copulation does, within the nest chamber.

Copulation

I have observed a number of apparently promiscuous copulations. At two different times dead Bank Swallows lying at the foot of the bank have been mounted repeatedly by several birds in quick succession in apparent attempted copulation, in one instance giving rise to an orgy of mountings

both of the dead bird and of other copulating birds. A stuffed and mounted Bank Swallow skin placed on the ground likewise elicited many copulatory attempts, but no evidence of semen emission was found on the dummy.

On May 22, 1950, similar quick mountings were observed among a group of birds dusting on a dirt road 50 yards from the colony site at Nine Springs Creek. However, I have never observed copulation in a known or apparently mated pair of Bank Swallows and because of the absence of observations it seems likely that it takes place in the nesting chamber as Emlen (1954) described in the Cliff Swallow (*Petrochelidon pyrrhonota*).

Watson (1946) describes copulation of Sand Martins observed along a road in mid-June. Both the paired birds were crouched low and motionless with bills and heads touching the ground until the male, with his wings waving wildly and his body swaying from side to side, walked toward the female. He mounted her back and the female's wings were raised in a taut curve while coition took place. Then the female shook herself vigorously and both birds flew away. Watson's detailed description of this act implies a deliberateness not apparent in the copulations I have observed.

Burrow Excavation

Once pairing is accomplished the digging of the burrow or rehabilitation of an old burrow usually proceeds rapidly during favorable weather. The work is shared about equally by male and female. Unpaired birds may scratch briefly and intermittently in their defended niches, enlarging their footholds, but no bird without a mate was seen to dig more than a shallow hollow.

Rehabilitation of an old burrow sometimes consists of cleaning the burrow and removing old nesting materials from the nest chamber. In one case eggs left from the previous year were pushed out of the burrow along with newly-loosened dirt before the burrow was re-used. More frequently the burrow is dug deeper and a new chamber excavated. As the freshly-loosened sand is pushed out, the old nest and cavity become covered and partially filled.

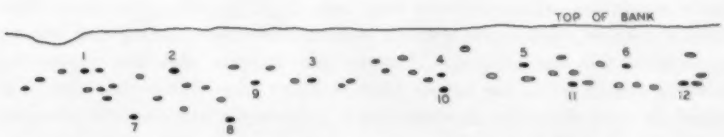

Fig. 3. Diagram of a portion of a Bank Swallow colony indicating by solid symbols burrows of which the rate of excavation is known. Burrows 1–6 are in locations above, and burrows 7–12 are in locations below others excavated at about the same time. Refer to Table 2 and Fig. 4.

TABLE 2

PROGRESS OF BURROW EXCAVATION

In burrows located in positions above others at same stage:

Date	Burrow Depth†					
	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5	Nest 6
May 9		* 1				
10	5	8	8		* 1	
11	10	14	13		7½	
12	14	16	17		13	
13	18	17	20	* 3	18	* 3
14						
15	19	19 (7)	20	20	21 (6)	13
16						
17						
18	19	19	20	21 (6)	21	18 (6)
19	19	19	20	21	21	18

In burrows located in positions lower than others at same stage:

Date	Burrow Depth†					
	Nest 7	Nest 8	Nest 9	Nest 10	Nest 11	Nest 12
May 10	* 1	* 1	* 1	* ½	* 2½	* 1
11	1	1	1	1	3	1
12	2	1½	5	1½	9	1
13	2	2	11	2	16	3
14						
15	2	4	22 (6)	5½	21 (6)	15
16						
17						
18	16	11	22	19	21	21 (9)
19	19 (10)	16 (10)		21 (10)	21	21

*Digging started during preceding 24 hours.

†Underlined depth is earliest record of maximum depth in each burrow. Number in parentheses is number of days of digging to attain maximum depth.

If the chosen site is a smooth, newly-exposed surface and affords no projections on which to stand, the bird clings to any slight irregularity of the bank, with the tail and sometimes the wings spread to help support it while scratching with a side to side motion of the bill. The mate often takes a position close beside with an outstretched wing covering and helping to support the one digging. It sometimes appears that this supporting position results when the second bird lands so close to the first that it is unable to close the wing; nevertheless, it undoubtedly aids the bird occupied in digging to hold its position.

As soon as a narrow ledge has been scratched out, the birds support themselves on it in a horizontal position on one foot and frequently with the outer wing widespread against the bank below, while scratching out

the beginning of the burrow with the upper foot. Both mates seem eager to take part in the digging, and they exchange positions at short intervals, the arriving bird often forcing his way inside and thus displacing the one at work.

The dirt is kicked back out of the opening with the feet. When the burrow becomes deeper, a shower of sand is sent back out of the burrow at each step of the entering birds, suggestive of a dog digging a deep hole. Contrary to popular opinion (Dawson, 1903; Forbush, 1929) dirt is not carried out in the mouth. I have frequently seen a Bank Swallow on leaving a burrow during the digging stage pick up a grain of sand in its bill and carry it away. This is commoner late in the nesting cycle and would seem to be a nest-cleaning activity.

As noted earlier, territorial defense, like digging, is shared by both members of the pair. The bird which is not engaged in digging is usually busy defending the site and frequently progress of excavation is interrupted when both members of a pair are involved in territorial defense. This is especially evident during the early stages of excavation.

When the burrow is very shallow, defensive threats are given while the swallows are clinging vertically to the bank, but as soon as the burrow is deep enough to accommodate both birds, the defender usually stands in the mouth of the burrow facing out. From this position the vocal threats and pushes are more effectively directed at intruders in positions below or to either side of the burrow, than toward those above the opening. Thus, in effect, higher positions become dominant to those below.

During the days when many pairs are starting their burrows, territorial threats and evictions occupy much of the time of the diggers, especially those occupying the more vulnerable low sites. Birds taking up sites in dominant positions above other territories are relatively free from chal-

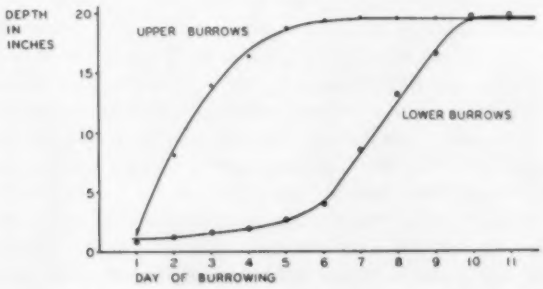

FIG. 4. Progress of burrow excavation. Dots represent mean depths of burrows 7–12 in Fig. 3 and Table 2.

FIG. 5. A Bank Swallow colony in a newly-excavated sand pit at Madison, Wisconsin. Burrows tend to be concentrated near the top of a high bank.

lenging attacks. As a result, burrows located high in relation to surrounding burrows increase rapidly in depth from the first foothold, while the excavation of low burrows is retarded for from two to five days until the hole becomes deep enough for one bird to dig undisturbed (Figs. 3 and 4; Table 2). Once a burrow is about three inches deep, excavation proceeds at a fairly uniform rate of about five inches a day irrespective of its position in the colony.

Thus, high positions would seem to be more favorable than low positions for establishing territories and digging burrows. This may explain why as is commonly observed, on a high bank offering a wide vertical extent of possible sites, the colony tends to be rather high and incidentally is safer from human and animal predators (Fig. 5).

The distance between adjacent burrow openings is determined by the area which a pair can successfully defend. In Table 3 are shown distances between burrow openings (measured center to center) in a densely concentrated colony where the soil was essentially uniform through a vertical extent of eight feet. This colony (Fig. 6) was in a new site and all the burrows were dug in 1952. Minimum spacing of openings was four inches, a majority being from five to seven inches apart. Territory in Bank Swallows is functional in minimizing the chance that adjacent burrows will run together or that the walls between them will break. In every case I have found (14 records) where two or more burrows met, only one has been completed and used for nesting. Stoner (1936) records instances of two nests located side by side in a common nest chamber after the thin

TABLE 3
MINIMUM DISTANCES BETWEEN BANK SWALLOW BURROWS

Distance to nearest burrow in inches	Frequency			
	From HIGH burrows	From MIDDLE burrows	From LOW burrows	Totals
4	2			2
5	10		7	17
6	6	3	2	11
7	13	5	2	20
8	2	3	3	8
9		2	2	4
10		1	2	3
11	1		1	2
12	1		3	4
..				
17			1	1
Total frequencies...	35	14	23	72
Mean distances....	6.4	7.5	8.1	7.3

partition between had broken down, but it is not stated at what stage the walls broke or whether either of such nests was deserted.

Positive social forces in a colony tend to keep the burrows concentrated. In locations providing extensive vertical banks that appear suitable for nesting, it is frequently found that one particular section is utilized by all or a vast majority of the birds. Adjacent sites having similar physical characteristics may remain untenanted. In several instances small groups of birds established territories at such nearby locations after nesting at the

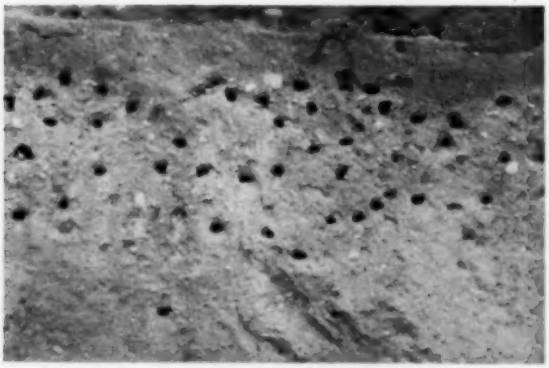

FIG. 6. Typical burrow spacing at a new site having a wide vertical extent of essentially uniform soil.

main site was well under way. Thus, at Nine Springs Creek in 1951 the traditional site near the road attracted the earliest birds of the colony. Next a small group of about 68 birds took up sites 350 yards upstream where only a couple of pairs nested in 1950. The latest nests were found in four smaller groups between these, where there had been no nesting in previous years. The spatial relationships of these sub-colonies with the number of nests and mean hatching dates in each are shown on the map of the colony (Fig. 7). Stoner (1941) has found by banding studies that the majority of breeding members of a colony reassemble in the same colony season after season.

It has been stated (Stoner, 1936; Bent, 1942) that burrows excavated in loose sandy soil tend to be deeper than those located in gravelly or clay banks. Although the banks used as colony sites in Dane County were fairly uniform in soil texture, a test of this correlation was made at 10 sites in eight colonies in Dane County. Samples were taken and analyzed for soil texture by the hydrometer method (Taylor, 1948). The results of these 10 analyses together with mean burrow depth in each location are shown in Table 4. Soil types varied from *sand* (94 per cent sand) to *sandy loam* (65 per cent sand, 35 per cent silt and clay). The percentages shown for soil textures are only roughly indicative of the degree of compactness, which is partially dependent on other factors. Nevertheless, a positive correlation was found between the mean burrow depths at each site, ranging from 20.4 to 36.2 inches, and per cent of sand in the soil. (The deep burrows at the Sprague-Dawley pit were a marked exception). At each of the colonies where

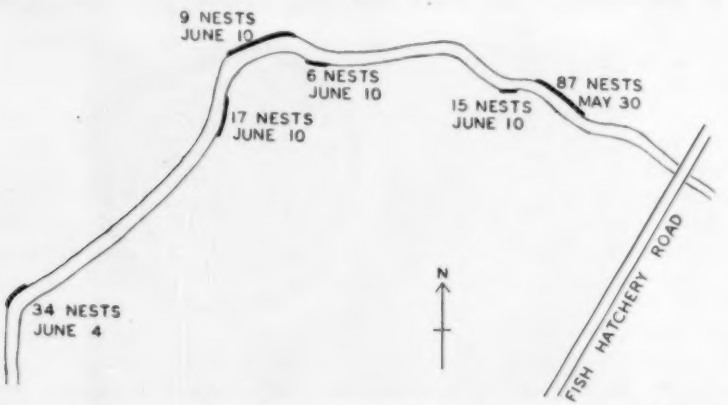

FIG. 7. Nine Springs Creek Colony. The number of nests and mean date of hatching in 1951 are given for each sub-colony.

TABLE 4
SOIL TEXTURE AND BURROW DEPTH

Colony	Mean burrow depth (inches)	Soil Texture		
		per cent sand	per cent fine material	Class
Wisconsin River, Area 1	36.2	92	8	Sand
Wisconsin River, Area 2	33.0	94	6	Sand
Columbia Co. V, Road cut	28.5	93	7	Coarse sand
Black Earth Creek, sandy layer	25.6	94	6	Coarse sand
Black Earth Creek, loamy layer	22.2	85	15	Loamy sand
Dane Co. Hwy. Q, Sand pit	21.6	85	15	Loamy sand
Monona Road cut, lower layer	24.2	83	17	Loamy sand
Monona Road cut, upper layer	20.4	80	20	Loamy sand
Nine Springs Creek	20.7	75	25	Sandy loam
Sprague-Dawley pit	26.5	65	35	Sandy loam

two distinct soil layers were used by the swallows (Black Earth Creek and Monona Road cut), burrows were deeper in the more sandy layer. As observed at these and other colonies where stratification occurs, a preference was shown for the more sandy layers and gravelly layers were avoided (Figs. 8 and 9).

Excavation of the nest chamber requires several days after the burrow has reached its maximum depth. The floor of the chamber is about two inches below the level of the burrow so that the completed nest and eggs are below burrow level. This was convenient for my observation with the Riparia-scope, since the eggs or newly hatched young were always well below the instrument where they could be clearly seen and not disturbed or damaged.

FIG. 8. Burrows in horizontal rows are excavated in thin layers of coarse sand in this old sand-pit, Racine County, Wisconsin.

FIG. 9. Bank Swallow excavations in coarse sand layers. Gravelly layers are avoided.

NEST BUILDING

Nest building begins as soon as the nest cavity has been excavated and both members of a pair contribute to its construction. Rather than "nest *building*" it might be more accurate to say "accumulation of nesting materials," for the nest is a somewhat formless mat of whatever materials are most readily obtainable. Fine grass blades and stems are the most common materials in most of the colonies where I have collected. Roots are torn from the eroding bank for use in nests, but the birds seem to prefer to use materials that can be picked up easily. Near farmyards straw is commonly used. The birds are quick to make use of any such materials dropped by others at the foot of the bank. At Nine Springs Creek I have watched Bank Swallows make repeated trips for dried grass from a roadway about 100 yards from the burrows.

The mat is about an inch thick in the middle and thinner toward the edges, conforming to the saucer-form of the chamber floor. When the eggs are laid it is loose and flat-topped. As incubation proceeds the center becomes depressed into a shallow hollow. A lining of feathers is added to the nest during incubation. Feathers, like grass, are brought to the nest by both members of the pair. As the lining is added the eggs are, of course, kept on top of the feathers.

Of thirty nests where the condition of feathering was noted and the stage of egg-laying or incubation known, only one contained a feather before egg-laying was completed and three nests still had no feathers after five and six days of incubation. Usually the first feathers are brought in on the second or third day of incubation and the nest is well lined with feathers

TABLE 5
CLUTCH SIZE IN THE BANK SWALLOW

Size of Clutch	Frequency		
	Before June 15	After June 15	Totals
2	–	2	2
3	3	1	4
4	14	13	27
5	64	5	69
6	23	–	23
Totals	104	21	125
Mean clutch size	5.0	4.0	4.8

before the eggs hatch. In a few instances I have seen feathers brought to the nest after the nestlings are a week old.

With few exceptions white chicken feathers were used, but colored feathers have also been noted. The number of feathers brought to the nests is much greater in colonies adjacent to chicken yards.

Stealing of feathers from nests left unattended was a common practice at the Nine Springs Creek colony.

EGG-LAYING

Observations with the Ripariascope indicate that eggs are laid at the rate of one per day until the clutch is complete. Data on clutch size obtained in this study are summarized in Table 5 and compared with reports from the literature in Table 6. In 125 completed clutches, I found the usual number of eggs to be five, although clutches of four and six eggs are not uncommon and a small number of clutches of two and three eggs were found being incubated.

I have no records of second nestings in this locality. Clutches started after June 15 were known to be or could be attributed to re-nestings of birds whose first nest was destroyed, usually by slumping of the bank. In one colony under daily observation, marked individuals in a re-nesting attempt took over a burrow recently left vacant by the brood of another pair. In some cases where re-nesting birds utilized old burrows, these were cleaned or dug deeper and a new nest built. In at least one instance a new clutch of eggs was laid in a dirty nest from which a brood recently fledged and to which no new nesting material had been added. The latest date I have found for the starting of a clutch was July 5, 1950. Mean size of clutches laid after June 15, and believed to be re-nesting attempts, was 4.0 eggs as compared with 5.0 eggs in first clutches (Table 5).

Stoner (1936) states that very few birds (his figures suggest about four

per cent) rear second broods. His assertion that the second broods are raised is based on one or more observations of a second clutch of eggs in a burrow from which young were fledged earlier in the same season. In the light of my observations this interpretation appears unwarranted. Unfortunately Stoner's statements were misconstrued when Gross (Bent, 1942) says that Stoner "presents concrete evidence that two broods are the usual thing in the colonies studied intensively by him."

Wilson (1812) makes the general statement that the Bank Swallow commonly has two broods. Audubon (1840) says that this species "generally rears two, and sometimes three broods in a season" in Louisiana, produces two broods in Kentucky, and "lays only once" in Newfoundland and Labrador. I was able to find no recent observations to confirm these statements. Oberholser (1938) states that there is "no definite nesting record for Louisiana."

Incubation

That incubation usually begins before the clutch is complete is evident from the variation of stages of development found within single clutches of eggs or broods of nestlings. Nearly every clutch, even those just completed showed a difference in apparent age of two to three days between the embryos of greatest and least development. In about two out of 31 instances the four or five embryos in one nest were at the same stage (day) of

Table 6
Reported Clutch Size in *Riparia riparia*

Authority	Locality	Clutch Size
Lack, D. (1947)	England	4–5
" "	Central Europe (Saxony)	5 (6)
" "	Eastern Galicia	5–6
" "	Norway	(4) 5 (6)
Forbush (1929)	New England States	3–7
Jourdain (in Witherby, *et al.*, 1940)	Great Britain	Usually 4–5 Sometimes 3, 6, or 7
Niethammer (1937)	Germany	5 (4–7)
Stoner (1936)	New York State	Early broods: 4 or 5 Late broods: 3 or 4
" "	Iowa	5 or 6 eggs (4 or 5 young)
Cory (1909)	Illinois and Wisconsin	3–6
Petersen (this study)	Dane County, Wis.	Before June 15: 5.0 After June 15: 4.0 Entire season: 4.8

TABLE 7
PRESENCE OF SEXES IN BURROWS AT NIGHT

Stage	Frequency*				Both sexes present	
	Total	Female alone	Male alone	Both sexes present	Female off first	Male off first
Nest-Building	4	1 (25)	1 (25)	2 (50)	2	0
Egg-laying	4	2 (50)	1 (25)	1 (25)	?	?
Incubation	32	21 (65.6)	2 (6.2)	9 (28.1)	3	6
Parental	36	23 (63.9)	6 (16.6)	7 (19.4)	4	3
Totals	76	47 (61.8)	10 (13.2)	19 (25)	9	9

*Actual number followed by percentage of total (in parentheses).

development and so had apparently been incubated an equal length of time. The extent of difference between oldest and youngest embryos in each clutch is not related to clutch size. It is evident therefore that incubation begins with the laying of the third, fourth, or fifth egg. Or it may be as Purchon (1948) found in the Swallow (*Hirundo r. rustica*) that incubation occurs for a short time each day from the laying of the first egg, and is increased each day until the maximum is reached. (In the case cited, incubation determined by day-long observations throughout the incubation period began with 10 per cent daytime incubation on the day the first egg was laid and increased to a maximum of 70 per cent daytime incubation on the eighth day.)

In two instances Stoner (1936) verified by dissection his observation that males were sitting on the eggs during daylight. By observation of marked birds I have found that the members of each pair share time on the eggs about equally during the daylight hours.

In Bank Swallows, as in most other passerines, only females develop an incubation patch. Ryves (1943) and Bailey (1952) believe an incubation patch is necessary for true incubation to occur and so consider that even in species in which males regularly take turns on the nest as in the Bank Swallow, males are incapable of true incubation. Bailey believes that in passerines the female alone will be found sitting on the eggs at night. My collecting records show (Table 7) that in 32 burrows from which I collected Bank Swallows during the incubation stage, the female was alone on the nest in 21 cases (65.6 per cent), both sexes were present in nine burrows (28.1 per cent) and in two instances (6.2 per cent) only the male of the pair was present in the burrow. In the nine instances where both sexes were present, the male left the nest before the female six times, and the female came off the nest first three times. It cannot be assumed however, that the incubating member of a pair will sit more assiduously.

Whether male Bank Swallows or any male passerines actually incubate, that is, raise the temperature of the eggs sufficiently to permit development of the embryos, can be positively determined only by studies of the egg temperatures produced by the males and the temperatures required for development.

In July, 1952, I placed the outdoor bulb of an Airguide indoor-outdoor thermometer among the eggs in a nest where the parent birds were color-marked for individual recognition. Access to the nest chamber was obtained by a hole dug behind the burrow. The thermometer scale was situated above the bank in such a manner that temperature readings could be made with binoculars from a blind while each entrance and exit at the burrow mouth could be observed.

In the first trial both birds deserted the nest. The second attempt was unsuccessful because the thermometer bulb was inadvertently pushed out of the nest. Results obtained in a third nest are shown in Figure 10. The female returned to the nest just once during the observation period and flew out with a feather almost immediately. During the next two and one half hours the male of the pair entered the burrow seven times for periods of two to 19 minutes, each time producing a sudden rapid increase in the nest temperature by as much as 21° F. above that of the unincubated nest. During the longer periods of 19, 17, and 18 minutes on the nest, temperatures of 94, 94, and 96 degrees F., respectively, were attained. Due to the size of the thermometer bulb (9 mm. diameter × 50 mm. in length) it was undoubtedly not covered as efficiently as a clutch of eggs alone would be. In normal incubation there is direct changeover between the members of a pair at the nest, so that eggs would not be subjected to periods of cooling between spells of incubation. It remains for further experiments of this type to provide temperature data of eggs incubated alternately by male and

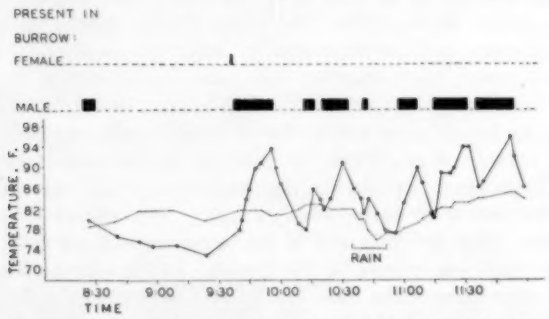

Fig. 10. Temperature of nest incubated by male Bank Swallow, July, 1952. Air (thin line) and nest temperatures were read from an Airguide indoor-outdoor thermometer.

TABLE 8
INCUBATION PERIOD IN THE BANK SWALLOW*

Clutch size	Total frequency	Class frequency		
		13 Days	14 Days	15 Days
3	1	–	–	1
4	2	–	1	1
5	2	–	2	–
6	6	3	1	2
Totals	11	3	4	4

*Days from laying of last egg to first egg hatching.

female. Nevertheless, the data presented here are positive evidence of male incubation.

The incubation period.—Incubation, from the laying of the last egg to the hatching of the last egg (when all eggs hatch), was determined in only two nests. It was found to be 15 days in both. In all nests the incubation period, counting from the laying of the last egg to first hatching, was from 13 to 15 days, as shown in Table 8. Evidence presented above indicates that incubation usually begins one or two days before the last egg is laid. Therefore it seems probable that the *actual* incubation period under natural conditions is 15 days, and apparent periods of 13 or 14 days occur when incubation begins two or one days, respectively, earlier than completion of the clutch.

Incubation periods recorded in the literature (Table 9) range from 12 to 16 days.

PARENTAL BEHAVIOR

Since incubation usually began one or two days before the laying of the last egg, hatching of a brood occurred over a period of two or three days and the young in each brood showed a difference of two or three days

TABLE 9
REPORTED INCUBATION PERIODS IN *Riparia riparia*

Authority	Incubation period
Evans (in Bergtold, 1917)	12 or 13 days
Burns, 1921	12 – 13 days
Stoner, 1936	14 – 16 days
Jourdain (in Witherby, *et al.*, 1940)	14 (12 – 16)
Niethammer, 1937	12 – 16
Baerg, 1931	13 – 14
Petersen (this study)	Apparent: 13 – 15 Actual: 15

in development. Egg shells were carried from the nest soon after hatching occurred. Three aspects of parental behavior are considered here: brooding, nest sanitation, and feeding.

Brooding.—The nestlings were brooded almost constantly on the day of hatching, the parents alternating on the nest. On successive days the amount of brooding decreased by a shortening of the length of each period on the nest. Six successive periods of brooding on one nest on the day of hatching were from seven to 28 minutes duration (28, **11**, 7, **10**, 7, **11**, periods by female in boldface). Two days later the same number of periods of brooding was observed per hour, but each period was only from three to five minutes long and longer periods of absence from the nest intervened. My observations do not substantiate Beyer's statement (1938) that the female does almost all of the brooding. His statement is based on his belief that he could distinguish between the sexes by the manner of movement of the birds. My birds were color-marked and the sexes known.

I have no observations on daytime brooding periods after the third day, but Beyer observed that by the seventh day brooding had practically stopped and the parent birds only occasionally sat on the young, usually for less than one minute at a time.

Until they are 10 days of age, the nestlings may be brooded by either or both parents at night. I collected the parent birds at night from 36 burrows containing nestlings (Table 7). The female was found alone on 23 nests, the male alone on six, and both male and female parents were present on seven nests. Observations of more than 100 nests at this stage indicates that the parents rarely spent the night in the nest after the young were 12 days old.

Nest Sanitation.—My observations agree with Beyer's finding that during the first days after hatching, the excrement of the nestling was swallowed. I have seen fecal sacs carried from the burrows when the nestlings were four days old. In the nest watched by Beyer all the excrement was carried away when the nestlings were seven days old and at nine days the young left the nest chamber to void in the burrows. I have observed that by 14 days they run almost to the burrow entrance and turn around to void. Bank Swallow nestlings never eject fecal sacs out of the burrow, so the ground below a colony does not become fouled with excrement as does the area below a Cliff Swallow colony.

Both parents assisted in nest sanitation. If excrement were present it was nearly always removed by the next bird leaving the burrow. Usually only one fecal sac was carried away at a time. If more than one was present, the bird did not return immediately for the second, but it was carried out after the next feeding.

There was a definite tendency for the parent birds to pick up *something* as they left the burrow. If no droppings were present, the birds would pick at or pick up a grain of sand or a tiny pebble as they ran out of the burrow.

Excrement is removed less promptly in the later stages of nestling life. Beyer reported that nest sanitation had stopped when the young were 17 days of age, but his observations continued for only an hour on that day. I have found that while the droppings may be left in the burrow for a time after 17 or 18 days, nest sanitation is usually resumed at irregular intervals until the young leave the burrow. In one instance a marked female returned to her own burrow and removed excrement left by her nestlings when they roosted there at 28 days of age.

Feeding.—My observations of feeding of Bank Swallow nestlings include data on six pairs of marked birds of known sex feeding broods in which the number and hatching date of the nestlings was known.

The mean feeding rate found in 33 nest-hours of observation (morning and mid-afternoon hours on fair, warm days) was 24.7 feedings hourly per nest. Marked differences are found in a comparison of feeding rates reported for this species from other localities during apparently similar weather (Table 10A). These differences are difficult to explain without more extensive study of feeding rates under varied conditions.

TABLE 10
NESTLING FEEDING RATES

A. Mean Hourly Feeding Rates.

Source of data	Locality	Hours of observation	Feeding rate
Petersen, this study	Wisconsin	33	24.7
Beyer, 1938	Ohio	2	24
Moreau and Moreau, 1939	England	24	33.3
Stoner and Stoner, 1941	New York	56	17.1

B. Feeding Rate and Brood Size.

Brood Size		Moreau	This study	Total
3	Hours observed	14	21	35
	Rate/nest	32.4	24.1	27.4
	Rate/nestling	10.8	8.0	9.1
4	Hours observed	10	12	22
	Rate/nest	34.7	25.7	29.8
	Rate/nestling	8.7	6.4	7.4

C. Feeding Rate of Sexes.

Number of pairs	Hours of observation	Feeding rate by male	Feeding rate by female	Total mean feeding rate
6	27	14.8	9.7	24.5

TABLE 11
FEEDING RATE AND NESTING AGE

This study			*Previous studies*			
Age	Hours observed	Feeding rate*	Age of nestlings	Hours observed	Feeding rate*	Reference
			3	2	24	Beyer, 1938
			2–4	14	14.1	Stoner, 1941
8	1	25	5–9	35	19.3	" "
9	2	19				
10	0	–				
11	3	20.7	10–12	7	18.3	" "
12	7	25.8				
13	14	30.5	13	2	28	Moreau and Moreau, 1939
14	3	24.7	14	2	44	" " " "
15	2	26				
16	1	24				
17	3	21				
18	7	22.4	"Nearly			
19	1	19	ready	20	32.8	" " " "
20	2	20.5	to fly"			

*Mean hourly feeding rate per brood.

My observations were spread over a number of days when the nestlings were from 8 to 20 days of age. The rates found for each day of nestling age (Table 11) indicate no trend during this span of nestling life. Data from other studies are presented in a parallel column, but since nestling age is not known exactly in all cases and conditions of time and locality are not uniform, detailed comparisons are not warranted.

The feeding rate at each nest was not proportionately greater in larger broods. Thus, the number of feedings per nestling was greater in smaller broods (Table 10B). In 35 hours of feeding broods of three nestlings (including data from Moreau and Moreau, 1939) the mean rates per hour were 27.4 feeding per nest or 9.1 feedings per nestling. Broods of four nestlings, observed for 22 hours were fed 29.8 times per hour, a mean of 7.4 feedings per nestling. The same relationship between feeding rate and brood size was found in Cliff Swallows (Petersen, MS), in the European Robin, *Erithacus rubecula*, (Lack and Silva, 1949), and Swift, *Apus apus*, (Lack and Lack, 1951).

Twenty-seven hours of observations of the six pairs in which the sex of each individual was known indicate that, as Beyer believed, males feed the nestlings more frequently than do females (Table 10C). The mean hourly feeding rate by males was 14.8, and that for females, 9.7, a total mean feeding rate of 24.5. Individual variation was noted, however, and it cannot be assumed that the bird feeding more frequently in any pair is the male.

Beyer noted during early days of nestling life as I found in older birds, that only one nestling was fed in each visit of the parents. A food call given by the adult bird as it enters the burrow is described by Beyer as a "series of particularly sweet fine notes higher in pitch than the usual Bank Swallow call." The nestlings were first heard to give a similar call at four days of age. I have found that nestlings will give this call whenever the burrow is partially darkened as though by an entering bird.

At nine days the nestlings rush toward the parent in the burrow to be fed. By 12 days of age the nestlings wait about six inches from the burrow entrance to be fed. During the last several days in the nest the fledglings are fed much of the time at the burrow entrance. Two to four or five birds sometimes jostle for front position in the burrow while waiting to be fed. When the parent approaches, each of the fledglings gives a series of loud sharp chirps, repeating it incessantly until he is fed, or until the adult bird leaves. After a young bird has been fed, he usually backs out of sight behind his mates or turns around and enters deeper into the burrow, giving up the front position to one of those who remain.

Eleven broods of nestling Bank Swallows were given color bands designating their home burrows. Eight of the female parents of these broods were individually marked. Observations of these birds indicate that young Bank Swallows fly from the burrows at about 20 days of age, but return to some burrow, frequently their own, during part of the day and for night roosting for several days. Nestlings as old as 28 days have been seen roosting in their own burrows.

The following observation suggests that the first flight of fledgling Bank Swallows may be brought about by a reduced feeding rate and by vocal urging of the parent birds. A marked adult male hovered in front of his own burrow where his three fledglings, 23 days old, were at the entrance calling and gaping. Presently he alighted at a neighboring hole a foot away, alternating his lower-pitched single note with the calls of the young birds. After perching less than a minute he flew back and forth in an area about 10 yards in diameter near the burrow entrance, continuing his low-pitched *buzz*, seemingly in answer to the continued begging of the young. Again he landed at a nearby burrow. This performance was repeated about 12 times in half an hour. Then one of the nestlings flew from the burrow in response to the alarm note of a bird flying overhead. During this period of observation, no food was brought to the nest, but three days later both parents were seen feeding one of the young that remained in or had returned to the burrow. Luring of the young from the nest by irregular or feint feeding or by calling has been reported by Nice (1943) in a number of

altricial species, including Barn (*Hirundo rustica*) and Tree (*Iridoprocne bicolor*) swallows.

Stoner (1942) found young Bank Swallows returning to their own or other burrows after their initial flights. My observations of feeding of marked fledglings (from 20 to 28 days old) by marked adults indicate that adult Bank Swallows recognize and will feed their own young which have returned either to their own or to other burrows. None of the marked adult birds was seen feeding a juvenile other than its own, even in the home burrow of the adult. Juveniles landing in a burrow not their own were in several instances attacked or pushed out by the adult resident. Nice (1943) notes that birds with altricial young do not recognize their eggs or nestlings, but that her Song Sparrows learned to recognize their young individually before independence was attained.

Post-nesting Behavior

At the Bank Swallow colonies I have observed, loafing sites such as nearby wires were used very little during the breeding season. At the time when young birds are leaving the nest, however, nearby wires are occupied for longer periods each day, and by increasing numbers of birds, both adult and immature.

During the first two weeks in August, 1950, small bands of recently-fledged young birds were seen on several occasions at the Nine Springs Creek colony engaged in entering holes, scratching at the bank and toying with nesting materials. On August 14 when several broods were still being fed in the burrows about 800 Bank Swallows, including a large proportion of juveniles, visited the colony. About 100 of these birds perched on wires near the bank, while others were engaged in cleaning and enlarging burrows or digging new holes. A constant twittering was heard from the birds. Such behavior suggests abortive nesting behavior.

During August, 1951, a group of post-nesting adults and juveniles was seen near a breeding site a mile west of Mazomanie. The birds sunned and dusted themselves on a long earth bank with a slope of about 30 degrees. Close observation showed that many of the birds were digging shallow holes, none exceeding five inches in depth. It is interesting that a slope unsuited as a breeding site should nevertheless be used for this post-nesting burrowing activity. Stoner (1936) observed post-season burrow-digging by juveniles at some of his colonies in New York State.

In a migrating flock of 2,000 Bank Swallows seen on September 13, 1945, Thom (1947) observed frequent attempted copulation and "threat displays." I saw similar attempted copulations among swallows in a small flock on a road in late July, 1952. I could not detect whether any of the individuals taking part in this activity were juveniles.

The annual appearance of huge flocks of Bank Swallows at traditional roosting sites has been described for a number of localities. Abby F. C. Bates (1895) described the activities at such a roost near Waterville, Maine. O. Widman (1907) states that such flocks begin to accumulate in the Mississippi River bottoms at St. Louis, Missouri, as early as July 1 and that migration continues throughout the month of August, all the birds having left by mid-September. Flocks of Bank, Tree, and Barn Swallows have been described by E. J. Sawyer (1918) in Jefferson County, New York. The largest Bank Swallow flock recorded was one near Toledo, Ohio, in 1931, estimated by Louis Campbell (1932) to include 250,000 birds.

The largest concentration of Bank Swallows I have observed was the flock of 800 that visited the Nine Springs Creek colony site in August, 1950. A group of about 700 birds spent several days in July, 1950, on the Mendota State Hospital farm near the north tip of Lake Mendota. Most of the birds perched along the wires or in large willow trees near the road, but several hundred sunned themselves on the bituminous-surfaced road. This location annually attracts such post-breeding flocks.

In the years 1950 through 1952 all the Bank Swallows had migrated from the Madison region by September 1. Schorger (1931) states that while Bank Swallows usually have migrated from the Madison area by September 1, some individuals may remain into September. The latest date for the species in his records is September 11.

II. Physiological and Morphological Cycles

Procedures for Collection and Autopsy of Specimens

For the study of the physiological and morphological cycles, adult Bank Swallows were collected from their burrows at night throughout the breeding season. A total of 114 adults (79 females and 35 males) was collected during the two years, 1950 and 1951. These were representative of all stages of the behavior cycle from burrowing to late parental stages (Table 12).

Table 12
Numbers of Specimens Collected

Phase of Cycle	Females	Males	Totals
Burrowing	2	0	2
Nest-building	11	8	19
Egg-laying	7	4	11
Incubation	28	10	38
Parental	31	13	44
Totals	79	35	114

After the birds had retired to their burrows for the night and darkness had fallen a number of burrows sufficient to provide the specimens needed were plugged with paper, so that our activities at the bank would not put these birds to flight. Then one burrow at a time was opened and the birds attracted to a flashlight at the entrance where they were captured by hand. Each specimen or pair of specimens was autopsied immediately before another was taken. It was found that specimens could be handled most advantageously by two people working together, one at the bank obtaining the birds and nest contents, and the other doing the autopsy in a laboratory set up in the back of a panel truck. The procedure used for each bird was as follows:

1. The adult bird was taken from the burrow and handed to the laboratory man for autopsy. Meanwhile the bank man measured the burrow, noted the condition of the nest, and collected the eggs and young, which were preserved in 10 per cent formalin for later examination.
2. The specimen was killed as quickly as possible by decapitation and the blood which flowed from the carotid vessels collected into a centrifuge tube.
3. A 0.02 ml. sample of blood was pipetted into 5 ml. of dilute tungstic acid in another centrifuge tube for later glucose determination. The pipette was rinsed with the dilute tungstic acid, then the tubes were corked and the pipette prepared for the next sample by rinsing successively in water, ethyl alcohol, and ether.
4. The bird was weighed on a triple beam balance.
5. The brood patch or ventral apterium was removed by dissection and preserved in Mossman's FAA fixative.
6. The body cavity was opened and the lower back region containing the testes or ovary and oviduct, was removed and preserved in FAA fixative.

The blood samples for glucose determination were refrigerated until the test was run the following morning. The whole-blood sample was frozen for later determination of serum calcium. The preserved organs were held for subsequent measurement and examination.

Determination of Reproductive Stages

The *phase* of reproduction of each specimen was readily noted by examination of the burrow or its contents. Thus, the following phases are represented by specimens: (1) burrowing, (2) nest building, (3) egg laying, (4) incubation, and (5) parental phase. Within each phase criteria were established as described below for determining the more precise reproductive *stage*.

Burrowing.—Only two specimens were secured before the start of nest building and these were from a late stage of burrowing.

TABLE 13
NEST BUILDING STAGES

Stage (Day)	As Determined by Ovary Condition:	As Determined by Nest Condition:
1	No ova over 2 mm. in diameter.	Few bits of nesting material.
2	Largest ovum 2 to 5 mm. in diameter.	Small amount of nesting material.
3	Largest ovum 5 to 8 mm. in diameter.	Moderate amount of nesting material.
4	Largest ovum over 8 mm. in diameter. No ova in oviduct.	Large amount of nesting material.
5	First ovum in oviduct.	Nest apparently complete.

Nest building.—Five stages of nest building were designated (Table 13). In female specimens, the development of the ovary took precedence over condition of the nest in determining the stage since the ovary more accurately indicates time before start of the egg-laying phase. Males collected with their mates were placed in the stage determined by the ovary condition of the female. Reproductive stages of males collected alone during this phase were determined solely by condition of the nest. Nest building does not proceed at a uniform rate in all pairs. Consequently the intervals between stages of nest building are not strictly uniform, although stages 2, 3, 4, and 5 as determined by ovary development do correspond approximately to days.

Egg laying.—Stages of egg-laying correspond to the number of eggs laid, except that where examination of ovary and oviduct indicated that a clutch was complete with less than five eggs (the most frequent number) it was placed in stage 5 of egg laying.

Incubation.—Stages of incubation of collected adult specimens were determined by the stage of development of the embryos measured in days, based on a series of embryos taken after known periods of natural incubation (Petersen, MS). Complications were presented by the fact that embryos in any one nest usually showed a range of development equivalent to two or three days of incubation. Adult specimens were assigned arbitrarily to the stage represented by the youngest or least-developed embryo.

Parental phase.—During the parental phase the specific stage to which each specimen was assigned is equivalent to the determined age of its youngest nestling. In order to establish criteria for aging nestling Bank Swallows observations and measurements were made of nestlings of known age.

The most apparent physical changes in young Bank Swallows during the nestling period are changes in weight and the development of plumage (Fig. 11).

The daily increase in weight for the first 11 days is so great that an average daily weight curve is useful in aging nestlings during this period. After the twelfth day the daily increment decreases until a maximum weight is attained on the fifteenth to seventeenth days, followed by a steady loss of weight to the day of fledging.

The most marked and easily observed feature of feather development is that of the ninth primary, which breaks through the skin on the seventh or eighth day and reaches a length of over 60 mm. at the time of fledging. The daily increment is so great that the length of the ninth primary becomes a useful aging criterion.

The ranges in weights on consecutive days overlap even during the first 12 days of development; likewise, the ranges of lengths of the ninth primary feathers on consecutive days overlap throughout their development. Consequently the age of nestling Bank Swallows as determined by these criteria is approximate and may be in error by one day in either direction.

Body Weight

The body weights of 121 Bank Swallows were obtained at autopsy throughout the breeding cycle. The mean weight of 82 females (Fig. 12) was 14.8 grams (range 11.4-18.5). Marked fluctuations were found during the cycle: (1) A rapid increase during late nest-building stages, paralleling the development of the ovary and oviduct, brought body weight to a maximum of 17.5 grams (mean weight of three individuals) on the day preceding laying of the first egg. This was an increase of 2.7 grams (18.2 per cent) above

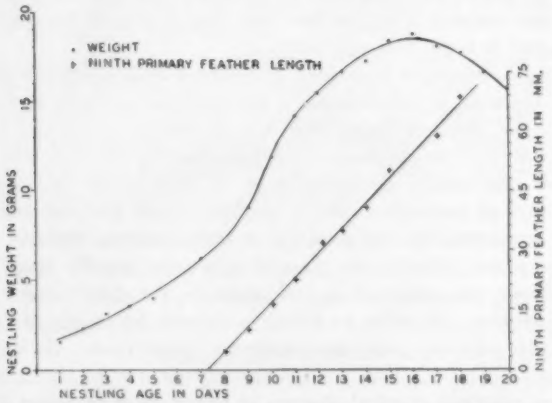

Fig. 11. Body weight and length of ninth primary feather in nestling Bank Swallows. During the first 11 days of nestling life, body weight was used as an aging criterion. Length of ninth primary feathers was used as an aging criterion for older nestlings.

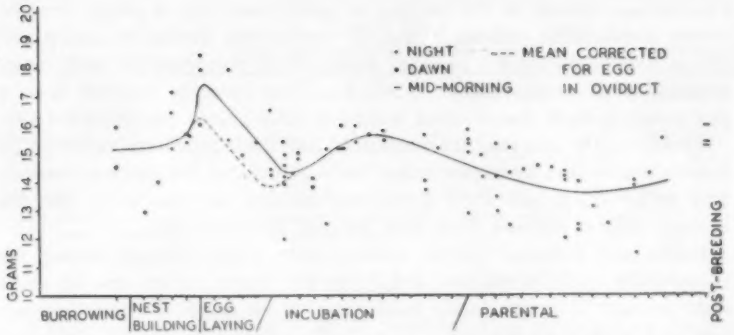

FIG. 12. Body weights of female Bank Swallows. In this and the following figures, the horizontal scale represents the sequence of stages in the breeding cycle.

the total mean weight. (2) During the egg-laying stage and the first day of the incubation phase the female body weight decreased to 14.2 grams. (3) An increase of about 10 per cent during the first half of the incubation period was followed by (4) a gradual decline beginning even before the parental phase. (5) The five specimens collected on the twelfth to fifteenth days of the parental phase suggest the beginning of a return to normal weight. Three individuals collected from post-breeding flocks averaged 15.6 grams (range 15.3–16.0).

The weights of 39 male specimens (Fig. 13) ranged from 11.8 to 16.1 grams with a mean of 13.7 grams, 1.1 grams less than the female body weight. While the difference in body weight between the sexes was greatest at the start of egg laying, females at any stage averaged heavier than males.

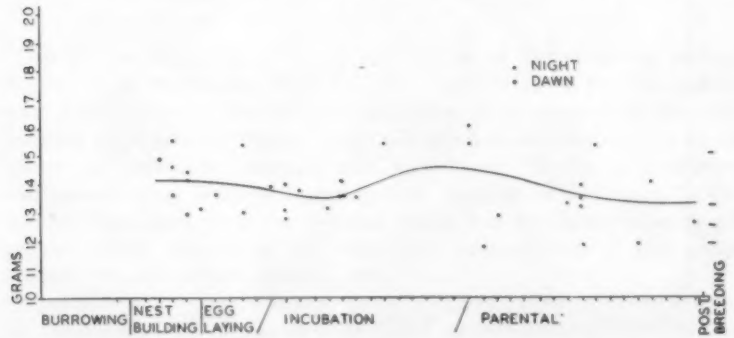

FIG. 13. Body weights of male Bank Swallows.

Fluctuations evident in the weights of males were (1) a slight decrease during nest-building and egg laying, (2) an increase during incubation and (3) a decline during the parental phase. Four post-breeding adult males averaged 13.25 grams (range 11.9-15.2). Nine juveniles collected from a post-breeding flock had a mean weight of 13.2 grams (range 11.6–14.9).

Stoner (1936) analyzed the weights of 249 Bank Swallows, including 22 known females and 13 known males. He reported that females were heavier than males (15.60 and 14.03 grams respectively) and also noted that the average weights declined from May through June and July.

Riddle and Braucher (1931) studied body weight changes during the reproductive cycle in pigeons and doves and found an increase of about eight per cent in weight during incubation. About one-third of this increase occurred in the crop-glands.

Baldwin and Kendeigh (1938) showed that the weights of birds characteristically increase during the day and decrease at night, being lowest at the beginning of each day's feeding activity. In this present study all weights were taken in the evening except a few which were obtained at dawn. These were found to average lower than evening weights during the same stage.

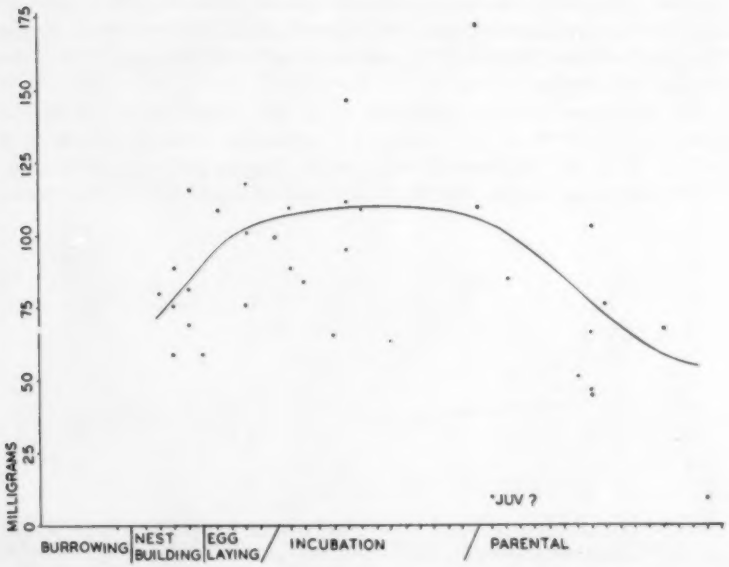

Fig. 14. Bank Swallow testis weights. See text for further explanation.

TABLE 14
BANK SWALLOW TESTIS WEIGHTS

Stage	Frequency	Mean weight	Range (mgm.)
Nest-building	8	78.9 mgm.	59.1–116.1
Egg-laying	4	107.5	80.6–133.5
Incubation	9 (10)	97.3 (87.8)	(2.5) 63.1–147.5
Parental: 1–3	3 (4)	120.0 (92.4)	(9.5) 85.8–163.7
Parental: 8–17	8 (9)	63.4 (57.4)	(9.2) 46.2–103.4

( ) Include three specimens of extremely small size.

TESTES

Weight.—Testes of 35 male Bank Swallows were preserved in fixative and later weighed on a torsion balance. Each of the weights plotted on the graph (Fig. 14) is the average of the two testes of a specimen, except for 10 birds in which one of the testes was used to prepare a smear. At any stage of the breeding cycle a wide range in testes weight was found (Table 14). Three birds had testes much smaller than any other birds so their testes weights (2.4, 9.4, and 9.2 mgm.) are parenthesized in the table.

Histology.—Specimens listed below, representative of each phase of the cycle, were sectioned in paraffin at eight microns and stained in iron hematoxylin and eosin:

Number	*Phase*	*Stage*	*Weight in milligrams*
1.	Nest-building	4	64.2
2.	Egg-laying	3	80.6
3.	Incubation	1	108.4
4.	Incubation	5	134.9
5.	Parental	1	164.5
6.	Parental	3	91.9
7.	Parental	9	44.6
8.	Parental	17	10.7

All of these testes, except no. 8, had bundles of mature sperms around Sertoli cells in the tubules (Stage 7 of Blanchard, 1941). A few free sperms were in the lumens of the seminiferous tubules of specimens from the nest-building and egg-laying stages. In the triangles between tubules large blood vessels and occasional interstitial cells were found. Tubules of incubation and parental stage testes had much greater numbers of free sperm in the lumens. Specimens from the parental stages had increasing amounts of cellular debris. Lumens of the testis from parental stage 9 were quite choked with debris and mature sperms.

Specimen no. 8 appeared to be in an advanced condition of regression. No spermatozoa or spermatids were found in any of the tubules of this testis. Only the basal layer of the tubule epithelium showed any organiza-

tion and lumens were filled with degenerating cells and cellular debris. The tunica albuginiae and tunicae propriae were several times thicker than any of the other testes sectioned and interstitial cells were relatively more numerous.

Ovary

The ovaries of female Bank Swallows were left *in situ* and preserved in fixative with the whole lower back regions. Later they were dissected, weighed, and examined for the number and size of their ova.

Each of the 79 ovaries collected (from burrowing through parental phases) contained a large number (estimated at from 50 to 60) of white ova of macroscopic size, under 1.5 mm. in diameter. During the four days preceding ovulation from four to six of these ova increased rapidly in size by deposition of yellow yolk. In domestic chickens (*Gallus gallus*) this increase begins 10 days before ovulation (Jull, 1952) and in the Domestic Pigeon (*Columba livia*), about four and one-half days (Riddle, 1916). In the Jackdaw (*Corvus monedula*) the period of rapid increase begins about four days before ovulation (Stieve, in Groebbels, 1937). The enlarged ova showed a distinct gradation in size in each ovary (Table 15). A study of the sequence of sizes together with the presence or absence of an egg in

Table 15

Weights of Ovaries and Sizes of Contained Ova

Specimen number	Stage	Weight of ovary (mgm.)	Size of enlarged ova (dia. in mm.)	Eggs in oviduct	Eggs in Nest
1	B	47.5	–	–	–
2	B	24.0	–	–	–
3	N1	22.0	–	–	–
4	N2	90.8	2, 4	–	–
5	N3	169.5	2, 2, 5	–	–
6	"	186.4	2, 2, 3, 5.5	–	–
7	"	140.0	2, 3, 6	–	–
8	N4	373.0	1.5, 2, 3, 5, 8	–	–
9	"	461.6	6, 8	–	–
10	"	778.3	5, 8, 9	–	–
11	N5	528.8	3, 6, 8	1	–
12	"	462.1	6, 8	1	–
13	"	480.2	3, 6, 8	1	–
14	E2	313.0	8	1	2
15	"	516.8	3, 4, 8	1	2
16	E4	49.6	–	1	3
17	"	40.9	–	1	4
18	E5	37.1	–	–	5
19	"	39.5	–	–	5
20	"	22.4	–	–	4
21–48	Incubation	Mean 31.3 (16.2–52.1)	–	–	3–6
49–79	Parental	Mean 22.4 (6.6–44.1)	–	–	Nestlings

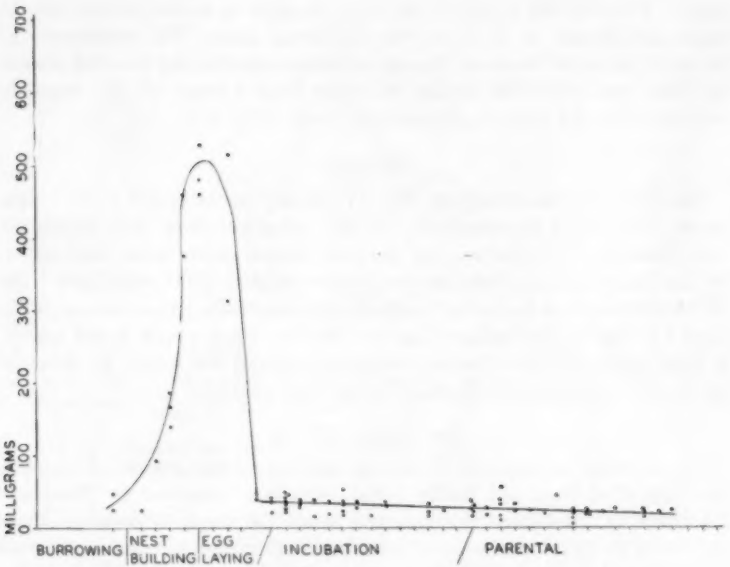

FIG. 15. Bank Swallow ovary weights.

th oviduct indicates that (1) an ovum was two to four mm. diameter on the second day preceding ovulation, (2) four to eight mm. diameter on the day preceding ovulation, and (3) eight or nine mm. diameter at ovulation.

Coincident with the rapid increase in ovum size, the weight of the ovary with ova included increased from about 30 milligrams to over 300 milligrams (Fig. 15). (Seven ovaries containing ova of ovulation size averaged 514.4

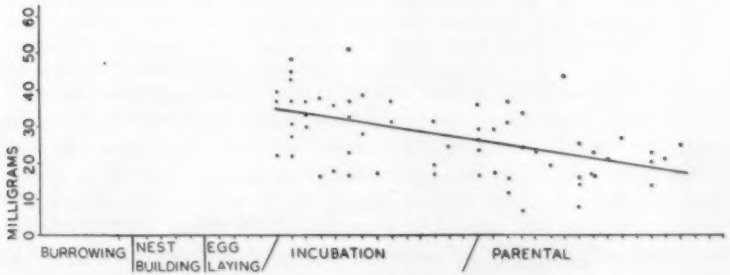

FIG. 16. Bank Swallow ovary weights. Data from specimens taken after egg-laying are repeated here on a greater scale.

mgm.) With the last ovulation the ovary dropped in weight to less than 53 mgm., and looked as it did in the burrowing phase. The appearance of the ovary remained the same throughout the incubation and parental phases, but there was a gradual decline in weight from a mean of 31.3 mgm. in incubation to 22.4 mgm. in the parental phase (Fig. 16).

Oviduct

The curve of oviduct weights (Fig. 17) is very similar to the ovary weight curve. The weight increased very rapidly for about three days before the first ovulation. This increase had probably started slowly some days earlier. By the beginning of ovulation the organs weighed 1500 milligrams. The decline in weight of the oviduct with the last oviposition (to a mean of 366.2 mgm.) is slightly less abrupt than the drop in ovary weight a day earlier. A more gradual decline during incubation reduced the weight to about 50 mgm., a level maintained through the parental phase.

Incubation Patch

The incubation patches of 75 females and the ventral apteria of 14 males were dissected from the freshly killed birds and preserved in Mossman's FAA fixative. Specimens representative of various stages in development or regression of the incubation patch were sectioned at eight microns and stained in iron hematoxylin or Mallory's stain for histological examination.

The four stages in the incubation cycle described by Bailey (1952) for

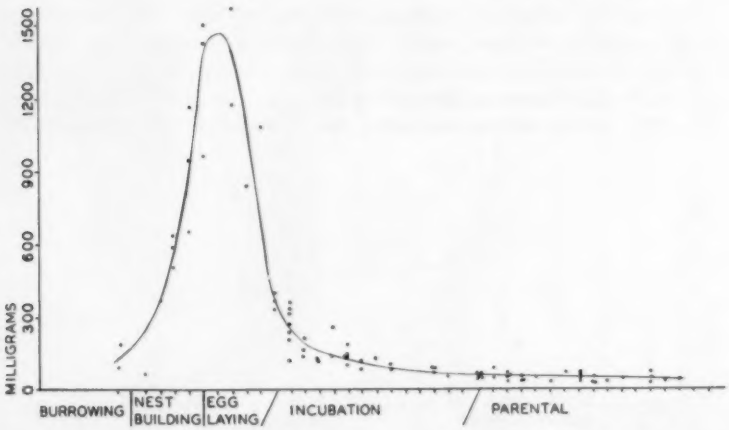

Fig. 17. Bank Swallow oviduct weights. Ova found in the oviducts during the egg-laying phase were removed before weighing.

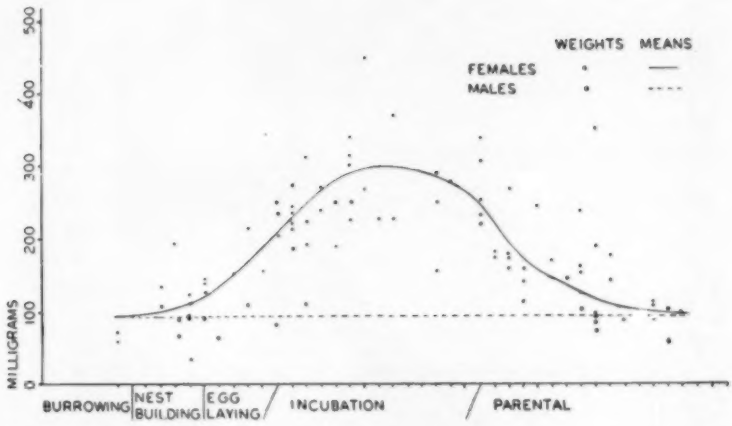

FIG. 18 Bank Swallow incubation patch weights. The open circles represent weights of ventral apteria of males, which do not develop an incubation patch.

the White-crowned Sparrow (*Zonotrichia leucophrys*) are recognized in the Bank Swallow. The following characteristics of each stage should be noted:

Stage I: Defeatherization.—This starts early in the nest-building phase and requires several days, being complete before the first egg is laid. According to Bailey the process is completed in 24 hours in the White-crowned Sparrow and Oregon Junco (*Junco oreganus*).

Stage II: Vascularization.—A remarkable development of the smooth muscle layer of the arteries not noted by Bailey suggests a possible increased development of vasomotor control of these vessels, which deserves further study. Development of such a regulatory mechanism in the incubation patch may have functional significance in conserving body heat while the female is off the egg.

Stage III: Edema.—Distension begins at the time of egg-laying in the lower dermis and as it increases, progresses toward the upper surface until at its maximum the entire dermis is edematous, limited only by a thin upper and basal membrane.

Stage IV: Recovery.—This change begins in the Bank Swallow several days before the eggs hatch, when the edema starts to subside slowly.

Before sectioning, each of the specimens collected was removed from the preserving fluid, rolled carefully on blotting paper to remove any excess of the fluid and weighed on a torsion balance. The weights (Fig. 18) correspond closely to the development and subsidence of edema. The ventral apteria of males underwent none of the changes evident in the females and maintained a uniform weight having a mean of 92.4 mgm. The incubation patches of females developed from apteria of about the same weight, and started to increase in weight during the nest-building phase. They had doubled in weight by the time egg-laying was completed and during the fifth to twelfth

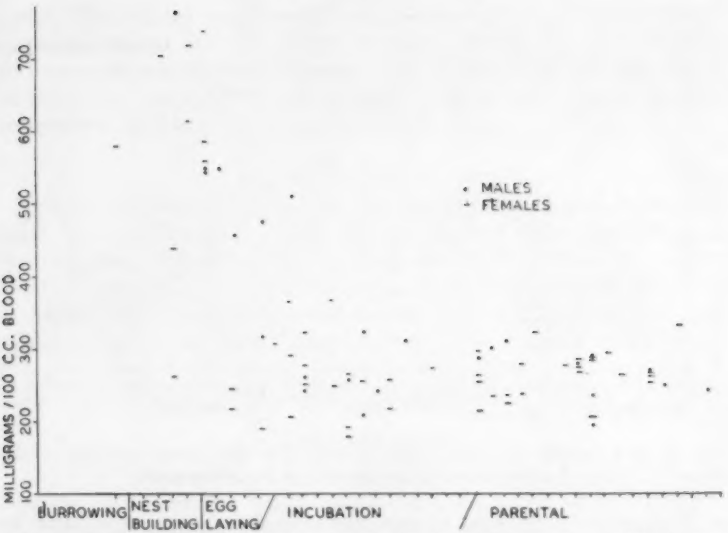

FIG. 19. Blood glucose concentrations in the Bank Swallow. Each symbol indicates the concentration in a single specimen. The mean for each phase of the breeding cycle is graphed in Fig. 20.

days of incubation, maintained a mean maximum weight of 281.0 mgm., about three times the original weight. When hatching began, a decrease in weight had started and by the time the nestlings were two weeks old, the apteria had returned to normal weight.

BLOOD GLUCOSE

Blood glucose determinations were made by Reinecke's (1942) method on 52 adult females and 25 adult males taken throughout the breeding cycle. The distribution of the individual values obtained are shown in Figure 19.

TABLE 16

BLOOD GLUCOSE CONCENTRATIONS (MGM./100CC.)

Phase in Cycle	Males			Females		
	N	Mean	95 per cent c.l.	N	Mean	95 per cent c.l.
Burrowing	–	–	–	1	582	–
Nest-building	4	601	175	8	579	135
Egg-laying	4	441	136	4	240	80
Incubation	7	263	37	15	264	32
Parental	10	266	25	24	268	12

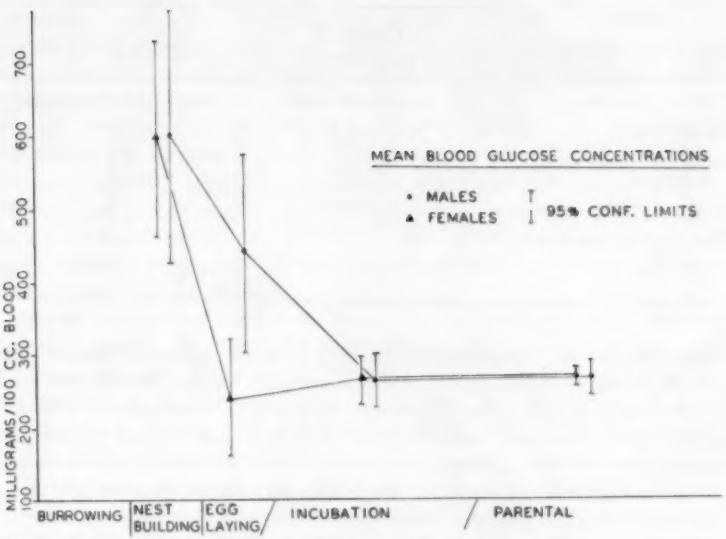

FIG. 20. Mean blood glucose concentrations in the Bank Swallow.

The means for each stage of the cycle are given in Table 16 and are graphed in Figure 20.

During incubation and feeding of young a mean level concentration of 266 mgm./100 cc. was found. Riddle and Honeywell (1924) found that most species of columbiform birds studied had a different and characteristic mean concentration of glucose (from 149 to 258 mgm./100 cc.) and Riddle (1937*b*) found that the concentration for pigeons was maintained at this normal level during incubation and feeding of young. It seems reasonable, therefore, that 266 mgm./100 cc. is the normal concentration for the Bank Swallow.

During the early stages of breeding activity, burrow digging and nest building, there was found in both sexes an elevation of 120 per cent above the level maintained during incubation and feeding of young. From this high the concentration dropped to the normal level quickly in the female and more gradually in the male. It may be conjectured that this striking elevation early in the breeding cycle is related to the high intensity of activity of the birds at that time. It seems probable that the behavior of the birds and the high concentration of blood glucose are both responses to the same hormonal stimuli. Riddle and Honeywell (1923) found a 20 per cent increase in blood sugar of pigeons with each ovulation period, beginning 108

TABLE 17
SERUM CALCIUM CONCENTRATIONS IN THE BANK SWALLOW

Age and Sex	Stage in Cycle	Serum Calcium (m. eq. Ca./l.)
Adult Female	Parental 7	4.9
" "	Parental 8	3.6
" "	Parental 9	3.6
" "	Parental 13	3.4
" "	Parental 14	3.6
" "	Parental 15	3.8
Nestling (undetermined sex)	—	3.6
		Mean....3.8

hours before and maintained at the high level throughout ovulation. The investigations of Riddle (1937) and his associates indicate that the hormonal mechanism of this glycemia is complex. At ovulation in the pigeons a marked hypertrophy of adrenal cortical tissue is found and cortical extracts are shown to moderately increase blood sugar. Prolactin likewise experimentally produces moderate glycemia. Evidence indicates further than an additional substance from the pituitary or adrenal may have a synergistic effect.

The more rapid return to normal apparent in females tested may be due to an increased rate of utilization of glucose associated with other activities including tissue growth in the oviduct and brood patch and deposition of food stores in the eggs by the ovary and oviduct.

SERUM CALCIUM

The method of Sendroy (1942) for photoelectric determination of serum calcium in small quantities of blood was adapted with a modification in the colorimeter filter and light source recommended by W. H. Schaeffer of the Rubicon Company (personal letter). The data obtained are presented in Table 17 but are insufficient for consideration of cyclic changes.

III. CORRELATION OF BEHAVIOR AND PHYSIOLOGICAL CYCLES

A review of the main features of seasonal reproductive cycles in birds seems pertinent before examining the behavior and physiological cycle in the Bank Swallow.

The anterior lobe of the pituitary gland, under the influence of some seasonal environmental factor (such as amount of daylight or temperature) produces gonadotropic hormones which bring the testes and ovaries into breeding condition. In both sexes, two distinct gonadotropic hormones, having separate effects on the gonads, are found. Follicle-stimulating hormone (FSH) brings about growth of ovarian follicles and in the male

stimulates development of spermatoza in the seminiferous tubules. An interstitial-cell-stimulating hormone (ICSH or LH) activates the interstitial cells of the testis to secretion of the male sex hormone, testosterone. ICSH is necessary for the production of the female sex hormones by the ovary. The sex hormones have the effects of stimulating development of accessory sex organs and secondary sexual characteristics and of initiating breeding behavior, including taking up of territories, mating, and possibly migration. Physiological effects shown for the female sex hormones, the estrogens, include elevation of calcium, fat, and glucose concentrations in the blood. Large amounts of estrogen have an inhibiting effect on the production of gonadotropins by the pituitary.

Another anterior pituitary hormone directly concerned in avian reproduction is prolactin. The effects of prolactin are initiation of broodiness and maternal behavior. Localized effects demonstrated for this hormone are proliferation of the crop-sac mucosa of pigeons (Riddle, Bates, and Lahr, 1935) and, in synergy with estrogen, the development of the brood patch in fringillids (Bailey, 1952).

The sequence of events in the behavior cycle of the Bank Swallow are brought together in Figure 21 and the factors of the physiological cycle in Figure 22. Physiological factors in the breeding cycle were not measured prior to the nest-building stage, but a brief review of the behavior in this period can be made.

Migration.—Determination of environmental factors effective in inducing migration in the Bank Swallow was not within the scope of this study. Observations were made, however, which indicated that once migration is underway, its rate is correlated with climatic factors. An apparent relationship was seen between time of arrival in the Madison area and temperatures prevailing for the preceding 15 days. Low temperatures may directly inhibit the migratory activity or may impede migration progress indirectly by causing a reduced food supply and necessitating longer periods of feeding. It was noted that activity upon arrival was influenced by weather conditions; fair weather with temperatures near or above normal appear to be necessary for taking up territories and associated behavior leading to pair formation.

Territorial and mating behavior.—On arrival at the breeding grounds the stage of gonadal development of Bank Swallows apparently places them in a disposition to take up territories and to mate.

Territorial behavior centers around a particular burrow. Both members of the pair identify themselves with the chosen site and defend it. The burrow screens much of the activity of the pair from other members of the colony. Thus the actual amount of territorial conflict is reduced, but the attachment to the chosen site is maintained throughout the breeding cycle, and is ex-

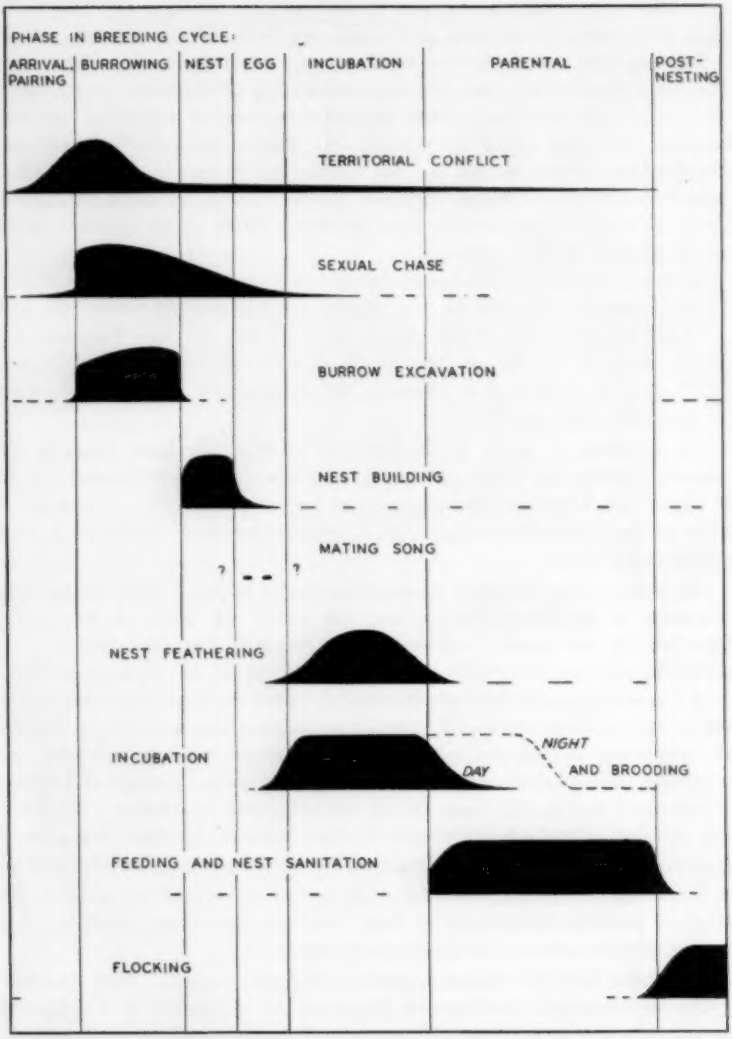

FIG. 21. Summary of behavior elements in the breeding cycle of the Bank Swallow.

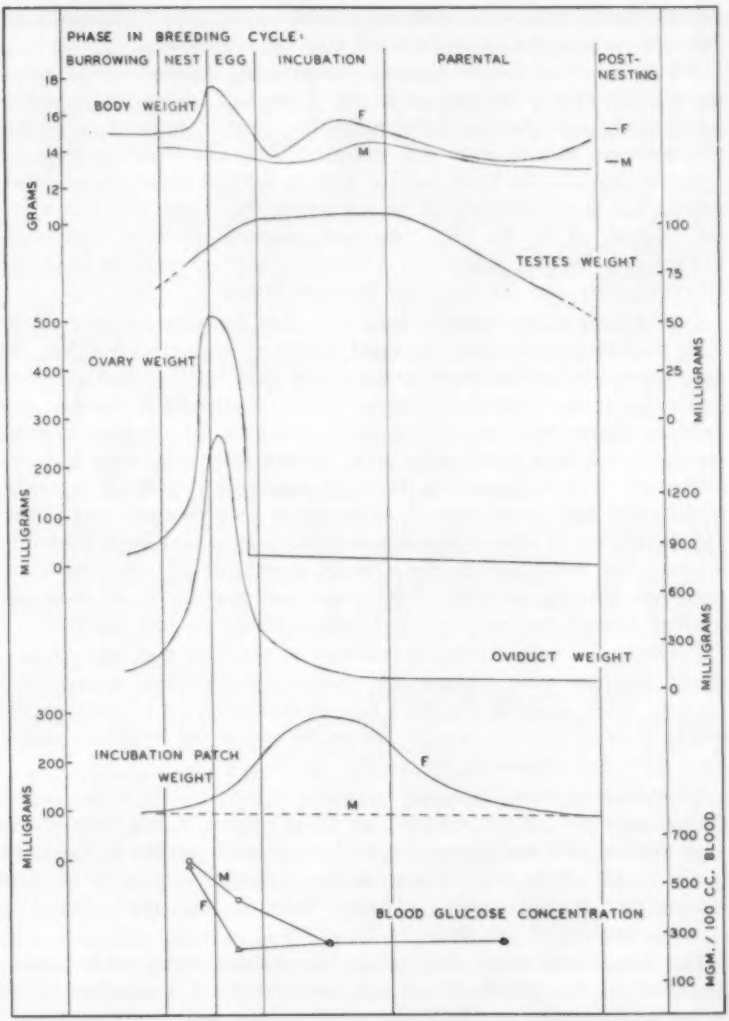

FIG. 22. Summary of physiological factors in the breeding cycle of the Bank Swallow.

pressed by territorial song, threat, or fighting whenever an intrusion occurs. As noted, birds failing to establish territories and obtain mates may leave a colony when breeding gets underway and take up sites in a different place. This also reduces the territorial conflict at the original site.

Mating in various species has been experimentally shown to occur following administration of testosterone in one (Emlen and Lorenz, 1942) or both members of a pair (Noble and Wurm, 1940*b*), or after treatment of one bird with androgen and the other with estrogen (Noble and Wurm, 1940*a*).

Sexual chase in the Bank Swallow is an activity of mated birds. Others join in, but in my observations, do not initiate the chase. This agrees with the findings of R. W. Nero (personal communication) in Red-winged Blackbirds (*Agelaius phoeniceus*). Burrow excavation likewise progresses effectively only after the pair-bond has been formed.

Burrowing and nest-building behavior.—Nest building behavior in the Bank Swallow coincides with the rapid growth of the ovarian follicles. The same correlation has been noted in the pigeon (Riddle, 1916) and Tricolored Red-wing, *Agelaius tricolor*, (Emlen, 1941). In the Bank Swallow nest-building cannot begin until a nest cavity has been excavated, so it seems necessary that some relationship exist between nest-cavity excavation and an internal condition preceding the rapid deposition of yolk. Two possible relationships may be conjectured, either one or both of which may obtain: (1) the activity of burrow and nest-cavity excavation may be motivated by developments which precede *rapid* ovum growth, or (2) excavation and associated behavior activities of the mated pair, such as sexual chase and territory defense, may serve as psychological stimuli for yolk deposition.

Development of the oviduct, as indicated by weight of that organ, follows closely after the ovary increase, but reaches a much higher weight (Note separate weight scales in Fig. 22). Egg production does not reduce oviduct weight as much as ovary weight, but by the end of the incubation period, the oviduct has returned to an inactive condition.

Copulation by mated birds was not observed but probably occurs at least during some part of the nest-building phase. Testes at this time contain large numbers of maturing sperm and relatively small numbers of free sperm in the lumens of the semeniferous tubules, indicating that as spermatozoa mature, they promptly leave the testes. Testes of later stages showed increasing numbers of free sperm in the lumens.

The sharp rise in female body weight in late nest-building can be entirely accounted for by growth of ova and the oviduct. A comparison of the weight of a complete clutch of eggs (7.36 gm. for an average clutch of 5 eggs) with the decrease of ovary weight during five ovulations (about 450 mgm.) and the difference in weight of pre- and post-oviposition oviducts

(over 1100 mgm.) indicates that over three-fourths of the material of the eggs is brought into the ovary and oviduct during the period of egg-laying. Relatively little of this comes from other body stores built up in advance, since the post-egg-laying body weight of the female is little lower than her weight before the rapid growth of the ovary.

The slight decline apparent in male body weights through the nest-building and egg-laying phases probably results from the high rate of activity during this period.

The relation of blood glucose concentrations in Bank Swallows to the breeding cycle is obviously not the same as in pigeons in which Riddle and Honeywell (1923) found a 20 per cent increase in blood glucose concentrations of females beginning 108 hours before ovulation and maintained at a high level throughout ovulation, but no change in males. The intense activity apparent in both sexes of the Bank Swallow during the early phases of the cycle indicates an energy utilization distinct from the subdued activity of the domestic pigeon. Some mechanism in the Bank Swallow provides for this need by maintaining blood glucose in both sexes at more than double the usual concentrations. The concentration in egg-laying females returns to an apparently "normal" level. In the incubation and parental phases the blood glucose level is relatively stable in both sexes.

Incubation. In Bank Swallows incubation starts before egg-laying is completed and is the function of both sexes. Incubation and broody behavior have been stimulated in domestic hens by prolactin (Riddle, Bates, and Lahr, 1935). This action of prolactin is accentuated by pre-treatment with sex hormones (Collias, 1946), but is inhibited by a continuing high level of estrogens (Collias, 1940).

Bailey (1952) has shown in fringillids that full development of the incubation patch is due to the combined action of estrogen and prolactin. Estrogen causes vascularization and prolactin causes defeatherization and edema. Stresemann (1934) noted a correlation in many orders of birds between the presence of an incubation patch in either sex and the part played by that sex in incubation. Thus, in most orders, for example Colymbiformes, Procellariiformes, Columbiformes, and Piciformes, both sexes share in incubation and an incubation patch develops in both sexes. In Strigiformes, Falconiformes, and Trochilidae only the females incubate and have incubation patches. In Phalaropes only the males incubate and have patches. Among the passerines the only species in which the male is known to develop an incubation patch is the Clark Nutcracker, *Nucifraga columbiana*, (Mewaldt, 1952). Reasoning that the development of an incubation patch must have functional significance, and that the correlation in most orders between presence of an incubation patch and share of the sexes in incubation

must extend also to the Passeriformes, Bailey postulates that male passerines, even where they are known to sit regularly on the eggs, do not incubate. In the Bank Swallow, the male not only sits regularly on the eggs, but in some instances was found to do so at night, and produced a temperature far above the environmental temperature. Development of broody behavior in male Bank Swallows may reflect the presence of prolactin, which in the absence of estrogen fails to produce a brood patch.

Noble and Wurm (1940*b*) found that broody behavior of Black-crowned Night Heron chicks followed treatment with male sex hormone. It is not certain, however, whether this behavior was in response to the testosterone directly or whether the testosterone stimulated the pituitary to secrete prolactin which caused the appearance of the broodiness.

Body-weight in both sexes increases during incubation and begins to decline by the end of that period. The increase may be related to the rather sudden reduction in overall activity in sitting birds. Riddle and Braucher (1931) found that pigeons gain in weight during incubation even though consuming less food per day than at other periods. No data were obtained on the amount of feeding by Bank Swallows during incubation, to determine whether the noted reduction in weight at the end of the incubation period might be related to lowered food consumption.

Feathering of the nest coincides with incubation behavior. Probably the presence of eggs in the nest is an external condition necessary for seeking and carrying feathers to the nest. The variations noted in time and amount of nest feathering may be related to success in finding feathers.

Parental behavior. In Bank Swallows feeding of the young is a response to their own young in the nest or burrow, or later, outside their own burrow. Adults were never seen to feed juveniles other than their own, either in their own or in other burrows. How early in the nestling period they can distinguish their own from other young was not determined.

Emlen (1941) found that male Tricolored Red-wings will feed any young in their own nest at any time after laying has started, but that females will respond only after incubation has started. Emlen (*op. cit.*) and Tinbergen (1939) both noted an incompatibility between sexual and parental activity. This concurs with observations that sexual phases of behavior are under the influence of sex hormones, while parental behavior is induced by prolactin, the effects of which are inhibited by the sex hormones.

Summary

The purpose of this study was to analyse the behavior cycle and certain factors in the physiological cycle of a wild species of bird for correlations that might give insight into conditions that regulate breeding behavior as it occurs under natural conditions.

The Bank Swallow (*Riparia riparia*) was selected as the subject for this study because it breeds in the vicinity of Madison, Wisconsin, in large colonies and the nests are built in burrows from which the birds can be easily obtained.

The arrival dates in the Madison vicinity in the six years 1947–1952 range from April 19 to April 26. Arrival occurred before April 22 in years when the mean temperature of the preceding 15 days was above normal. Arrival was after April 22 when the mean temperature of the preceding 15 days was below normal.

The following sequence of events in pair formation was observed: an unpaired bird (probably the male) selected a burrow site, and defended it by vocal threats and physical force against intrusion. One among those which persistently returned to the defended site eventually was tolerated and became recognized by the bird holding the territory as his mate. Sexual chase and a rarely-heard mating song strengthen the pairing bond. Completed copulations were never observed and are thought to occur within the nest chamber.

Burrows were excavated only by mated birds and both members of the pair shared in the work. Excavation began slowly and erratically in burrow locations where much territorial fighting occurred. Once a burrow is about three inches deep, excavation proceeded at the rate of about five inches a day. A tendency was noted for burrows to be concentrated near the top of the bank. A positive correlation was found between amount of sand in the soil and burrow depth.

The nest chamber was usually supplied with a mat of grass, straw or roots before egg-laying began. A lining of feathers was added after the eggs were laid. Nesting materials were brought by both members of the pair.

Eggs were laid at the rate of one per day. No instances of second nestings were found in this study, but re-nestings following nest destruction were common. Mean size of first clutches was 5.0 eggs. Later clutches, believed to be re-nestings, averaged 4.0 eggs.

Incubation usually began one or two days before the clutch was completed. Contrary to generalizations made for passerine birds, males shared in incubation. An incubating male was found to raise the temperature of the eggs to 96°F., as much as 21°F. above the temperature of the unincubated nest. In two instances the male alone was found at night on nests containing eggs. The incubation period under natural conditions was found to be 15 days. Nestlings were brooded almost constantly on the day of hatching, but the amount of daytime brooding decreased rapidly during succeeding days. Both of the parents or either alone brood young nestlings at night,

but the parents were rarely found at night in burrows containing nestlings over 12 days old.

Nest sanitation was maintained throughout the nestling period. The mean hourly feeding rate found in 33 nest-hours of observation in fair weather was 24.7 feedings per nest. The feeding rate was not proportionately greater in larger broods so that the number of feedings per nestling was greater in smaller broods. Males fed the nestlings more frequently than did females. After 12 days of age nestlings are frequently fed at or near the entrance to the burrow. Observation of individually-marked parents feeding nestlings having colored leg bands designating their home burrow indicated that Bank Swallows can distinguish their own nestlings from others, and will feed only their own nestlings, even when they have left their own burrow and returned to the same or another burrow. The nestlings may fly from the burrow as early as 18 days if disturbed, but usually took their first flight at about 23 days of age. In several instances the young birds were lured from the nest by reduced feeding and by calling of the parents.

Abortive burrowing and nest-building was shown by post-breeding flocks of juveniles and adults.

Data on the morphological and physiological cycles were obtained from 79 females and 35 males collected from their burrows at night, together with the nest contents from which the stage of the birds was determined.

The mean body weight of females (14.8 grams) increased with growth of the ovarian follicles and oviduct preceding ovulation, decreased with egg-laying, rose during the first half of incubation, then declined again to the end of the breeding cycle. Mean weight of males (13.7 grams) showed a similar rise and decline in incubation and parental phases.

Testes were heaviest through the incubation period. Regression started early in the parental phase and in a specimen from the seventeenth day of the parental phase, an advanced condition of regression was found.

Ovaries increased tenfold in weight during the four days preceding the first ovulation. Ova were eight or nine millimeters in diameter when ovulation occurred. Oviduct weights increased at the same time as ovary weights and reached a peak of 1500 milligrams at the time of the first ovulation.

A study of the histological and weight changes in development and regression of the incubation patch in females indicated that defeatherization started in early nest-building and required several days; vascularization produced a remarkable development of the smooth muscle layer of the arteries. The weights corresponded closely to the increase and subsidence of edema. No such changes occurred in the ventral apteria of males.

During nest-building blood glucose concentrations of both sexes were more than double the normal level of 266 mgm./100 cc. found during incubation and parental phases.

Correlations between elements of the behavior and physiological cycles were noted and discussed and comparisons made with data on other species of birds.

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SEX AND AGE RATIOS OF SOME JAPANESE BIRDS

BY H. ELLIOTT McCLURE

OVER a period of more than two years, from July 1, 1950, to January 1, 1953, nearly 3,000 birds were collected in Japan, mainly by shooting (some were netted). Blood serum from these specimens was tested for neutralizing antibodies to Japanese B encephalitis virus. Since the presence of virus in mosquitoes is a midsummer phenomenon and the birds appeared to be more susceptible to attack by the virus when young, it became desirable to know when the avian population had the largest percentage of juveniles. During the period of active field work the interest lay in the collection of blood, and not particularly in the sex and age ratios of the birds. Every bird that passed before the gun was taken and, when feasible, this was continued with each species until 10 or more specimens were collected.

The object of this paper is to present the accumulated data without drawing generalizations upon the sex and age ratios of Japanese birds, since the number of specimens collected is too small in many cases. It was considered that the desired information concerning the period of greatest incidence of juveniles was obtained by a review of the age ratios of collected birds and by corollary studies of nesting species. The raw data are summarized here in order to make them available to other workers who might be engaged in investigations of age and sex ratios.

Most of the specimens were collected within a 40-mile radius of Tokyo. An additional series of several hundred was taken in Hokkaido, Northern Honshu, and in Kyushu. The habitats selected for collecting included tidal flats, marshlands, rice paddies, upland farms and forest. The upland habitat types were mixed deciduous-evergreen forest with the associated subdivisions. All of the habitats were dominated and greatly altered by man's activities.

Except where there were obvious plumage differences, such as those of the Gray Thrush (*Turdus cardis*), the sex was determined by dissection. Specimens of uncertain sex are not included in Table 1.

First-year passerine birds were separated from adults on the basis of cranial examination. Cranial "ossification" takes place rapidly in the passerine forms as demonstrated by Nero (1951. *Wilson Bull.*, 63:84–88). It progresses in a conspicuous pattern and usually is completed by midwinter. Only those individuals in which the cranium was examined are listed in Table 2.

Sex Ratios

In the present study 2,311 specimens of 183 species were sexed. The numbers examined each month were as follows: January, 97; February,

TABLE 1

MALE-FEMALE RATIO* OF ABUNDANT BIRDS OF JAPAN, BASED UPON SPECIMENS COLLECTED FROM JULY 1, 1950, TO JANUARY 1, 1953

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Snowy Egret (*Egretta garzetta garzetta*)	—	—	—	—	1:0	1:2	2:0	—	9:12	4:1	1:0	1:1	19:16
Lesser Egret (*Egretta intermedia intermedia*)	—	—	—	—	2:3	5:4	3:1	2:0	8:28	—	—	—	20:36
Black-crowned Night Heron (*Nycticorax nycticorax nycticorax*)	—	—	—	—	1:3	2:4	2:2	0:2	17:18	—	4:4	—	26:33
Kentish Plover (*Charadrius alexandrinus nihonensis*)	1:1	—	0:1	6:2	7:2	0:1	—	—	7:4	2:5	1:1	4:1	28:18
Common Sandpiper (*Actitis hypoleucos*)	—	—	3:2	3:3	—	—	—	1:1	5:6	2:1	—	—	14:13
Eastern Turtle Dove (*Streptopelia orientalis orientalis*)	1:1	0:1	1:0	5:0	0:1	—	—	6:6	0:1	0:3	1:1	1:0	15:14
Skylark (*Alauda arvensis*)	0:2	—	6:1	17:7	1:0	6:1	—	4:0	5:3	8:5	2:0	1:2	50:21
House Swallow (*Hirundo rustica*)	—	—	4:4	—	—	—	2:1	7:2	—	1:0	—	—	14:7
Thick-billed Crow (*Corvus levaillantii japonensis*)	0:1	—	4:2	1:4	—	0:1	—	1:0	—	8:6	2:3	—	16:17
Carrion Crow (*Corvus corone orientalis*)	—	—	3:7	4:5	—	—	1:0	—	1:0	5:9	4:6	—	19:27
Blue Magpie (*Cyanopica cyanus japonica*)	—	1:1	—	1:0	3:2	1:1	8:2	5:3	0:3	—	2:1	—	21:13
Japanese Jay (*Garrulus glandarius*)	—	0:1	1:0	0:1	—	—	—	—	1:0	16:9	6:0	2:0	26:11
Brown-eared Bulbul (*Ixos amaurotis*)	0:1	2:2	4:2	7:4	—	—	—	—	—	7:7	4:4	2:1	26:21
Dusky Thrush (*Turdus naumanni*)	5:3	2:1	2:6	5:6	—	—	—	—	—	—	3:4	1:1	18:21
Pied Wagtail (*Motacilla alba lugens*)	0:1	—	9:4	5:5	—	—	—	—	—	4:3	4:4	1:3	23:20
Bull-headed Shrike (*Lanius bucephalus bucephalus*)	2:0	0:1	5:0	4:1	—	0:1	0:1	0:1	3:4	7:2	1:0	0:3	22:14
Ashy Starling (*Sturnus cineraceus*)	4:3	1:0	7:4	11:11	3:3	5:6	17:11	32:4	22:16	12:4	2:2	4:5	119:69
Tree Sparrow (*Passer montanus*)	0:3	1:0	5:6	5:3	13:19	7:8	13:18	25:6	8:4	38:30	7:10	3:7	124:113
Oriental Greenfinch (*Chloris sinica*)	1:0	1:1	7:7	12:3	0:1	—	1:0	—	—	1:0	6:5	6:1	35:18
Meadow Bunting (*Emberiza cioides ciopsis*)	4:1	1:0	10:2	2:1	1:0	1:1	—	1:1	0:1	1:4	5:12	4:11	30:24
Male-female Ratio*	18:17	7:8	71:48	88:56	32:34	28:30	49:36	84:26	86:100	116:89	55:57	30:36	665:547
Ratio of males to 100 females	105	87	148	150	94	93	136	323	86	130	96	83	123

*Figures are the actual numbers examined.

32; March, 214; April, 264; May, 127; June, 135; July, 141; August, 149; September, 289; October, 417; November, 319; and December, 123. The sex ratio based upon the total specimens and for all species was 120 males to 100 females.

Based upon the total specimens collected each month the sex ratios, expressed as males per 100 females, were as follows: January, 100:100; February, 110:100; March, 130:100; April, 150:100; May, 130:100; June, 150:100; July, 130:100; August, 240:100; September, 83:100; October, 120:100; November, 100:100; and December, 110:100. For November, December, January, and February the ratio was 100:100. In March and April, when the males were setting up territories, were singing conspicuously and were collected easily, the observed ratio rose to 145:100. During May, June, and July, when the females were secretive and occupied with nesting, the ratio remained at 140:100. With the autumn influx of young into the population, the ratio rose to 240:100. Since males may be less secretive than females and juveniles probably are less wary than adults, the appearance of juveniles in the population might weight the collections toward males. This probably accounted for the preponderance of males in August. With dispersal and migration during September and October, the ratio returned nearly to equality. It is to be emphasized that these ratios represent only those existing in the collections made and are not necessarily those of the existing population. The sex ratios of the 20 species collected most commonly are listed in Table 1. The figures presented above include data from all the 183 species collected.

Age Ratios

Since many of the specimens collected were sent to museums and since ripping of the scalp would damage the skin, only 1906 passerines were examined for cranial ossification. The numbers of passerines examined each month were: January, 22; February, 13; March, 95; April, 105; May, 49; June, 41; July, 99; August, 225; September, 126; October, 211; November, 101; and December, 52. The ratios showing incomplete ossification (immature) to complete ossification (adult) among the passerines were as follows: January, 5:100; February, 0:100; March, 1:100; April, 0:100; May, 81:100; June, 70:100; July, 312:100; August, 450:100; September, 300:100; October, 174:100; November, 300:100; and December, 62:100. The percentages of incompletely ossified crania are given in Table 2. Both methods of presenting the data show a normal accession and recession of young birds in the population.

Many factors combine to produce this phenomenon, most conspicuous of which is the maturation of the crania. In some species early migration of

juveniles would affect the apparent age ratio, but for resident forms, the area under study in Japan was large enough to include the local movements of juveniles. A differential loss of individuals, greater in juveniles than in adults (Hickey, 1952. *Special Sci. Rept., Wildlife no. 15, U.S. Fish and Wildlife Serv.*), would affect the change in age ratios as well. However, because juveniles probably are less wary than adults, the data probably are weighted toward juveniles. In spite of these variables it is believed that the method used was of value in identifying the period when the habitats were permeated most heavily by birds of the year. Table 2 lists 12 of the passerine species collected in numbers greater than 25 and lists the actual numbers examined for age characters.

TABLE 2

ADULT—IMMATURE RATIOS OF SOME JAPANESE PASSERINES, BASED UPON SPECIMENS COLLECTED FROM JULY 1, 1950, TO JANUARY 1, 1953

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Skylark	2:0	—	9:0	24:0	1:0	4:2	—	3:1	8:0	10:4	2:0	3:0	66:7
House Swallow	—	—	8:0	—	—	0:1	1:1	6:30	—	0:1	—	—	15:33
Thick-billed Crow	1:0	—	6:0	5:0	—	0:1	—	1:3	—	11:4	5:0	—	29:8
Carrion Crow	—	—	10:0	10:0	—	—	0:1	0:4	1:2	10:6	5:5	1:0	37:18
Blue Magpie	—	2:0	—	1:0	5:0	2:0	5:11	4:11	0:9	2:3	1:6	—	22:40
Japanese Jay	—	1:0	1:0	1:0	—	—	—	—	0:1	6:18	2:4	2:0	13:23
Brown-eared Bulbul	1:0	4:0	8:0	11:0	—	—	—	—	—	11:5	1:9	3:0	39:14
Bull-headed Shrike	3:0	1:0	5:0	5:0	—	0:1	0:2	1:2	5:2	7:2	1:0	3:0	31:9
Ashy Starling	7:0	1:0	10:0	21:0	4:2	5:6	10:23	15:85	16:32	10:14	3:2	8:1	110:165
Tree Sparrow	3:0	1:0	12:1	8:0	16:19	11:6	8:36	9:46	1:43	8:72	2:22	4:10	83:254
Oriental Greenfinch	1:0	2:0	14:0	16:0	1:0	—	0:1	0:1	0:1	0:1	0:13	6:2	40:19
Meadow Bunting	4:1	1:0	11:0	3:0	0:1	2:0	—	2:1	1:4	2:4	3:15	2:7	31:33
Adult—Immature Ratio*	21:1	13:0	94:1	105:0	27:22	24:17	24:75	41:184	32:94	77:134	25:76	32:20	516:623
Per cent with Immature Cranial Characteristics	5	0	1	0	46	41	75	81	74	62	75	38	

*Figures are the actual numbers examined.

SUMMARY

From July 1, 1950, to January 1, 1953, nearly 3,000 birds were collected in Japan for serological study, and the majority were sexed and aged by dissection. The overall sex ratio was 120 males to 100 females. The ratio varied from month to month as changes in activities of each species changed their availability to the gun. The fall age ratio in passerines (based on ossification of the crania) was three immature birds per adult. Of 183 species collected, peak numbers of juveniles were taken in September. This peak came in August in the 12 most common passerine species.

DEPARTMENT OF VIRUS AND RICKETTSIAL DISEASES, 406TH MEDICAL GENERAL LABORATORY, APO 500, SAN FRANCISCO, CALIFORNIA, AUGUST 1, 1954

THE SUMMER SCHEDULE OF THE EASTERN WILLET IN GEORGIA

BY IVAN R. TOMKINS

THE Eastern Willet (*Catoptrophorus s. semipalmatus*) comes to the coast of Georgia in spring, breeds, and is gone again by midsummer. Its close relative, the Western Willet (*C. s. inornatus*), appears as a migrant in August and September, and again in February, and a few individuals may be seen at nearly any time of the year.

This paper deals mainly with the Eastern Willets which breed on the coast of Georgia and South Carolina. This population may exist as one distinct from other willet populations of the Atlantic coast. There are many questions concerning these willets which, to my mind, remain unanswered. Where they spend the winter, in what locality the molt takes place, and their appearance in winter plumage are some of these.

I have accumulated notes on this species for more than 30 years, giving enough time for checking various conclusions, and tending to reduce some errors of brief acquaintance. Most of my field work has been done in Chatham County, the most northerly of the coastal counties of Georgia, although it has reached out at times 100 miles northward into South Carolina and an equal distance southward.

Gilbert R. Rossignol has allowed me to use his egg records, covering collections made from 1907 until about 1937. I am indebted to him for this and other considerations.

The summer residence of the willets in our locality appears to be divided into: (*a*) courtship, about three to four weeks; (*b*) egg-laying and incubation, about four weeks; (*c*) care of young, not more than four weeks, or a residence of about three months.

The calendar of our local population may be summarized in this fashion: (*a*) spring arrival, March 7 through March 30; (*b*) establishment of territory, egg-laying and incubation, April 7 through July 7; (*c*) care of young, April 30 until about mid-July. This schedule is general only, based on the normal year. From the data assembled, there seems to be but one nesting each year, and I have made no observations that would indicate re-nesting if a clutch of eggs is destroyed.

ARRIVAL

The first willets arrive about March 7, and there is a full population by the end of March, although it is quite likely a few may arrive still later. I think they arrive at night, for I have heard their ringing courtship notes

in darkness prior to the observed arrival of the first individuals. I have seen no evidence of transient flocks bound elsewhere. The birds arrive in well-worn, speckled plumage and courtship is begun (or resumed) at once. For some weeks the willets flock along the shell-banks and reefs of the salt marshes, and on the sand-mud flats, but they are not found on the higher grassy areas where the nests will be abundant later. Flocks of 30 or more are common. In Glynn County, Georgia, on March 24, 1938, I counted 138 birds on a sand-mud flat, some of them feeding, others engaged in courtship activities. On April 6, 1938, in the same place I counted 80 willets.

Though a few nests are found in early April, there seems to be a mass movement onto the nesting grounds about April 20. E. Burnham Chamberlain and I drove through several miles of willet nesting habitat on April 22, 1950, and saw very few birds. The next morning we drove the same route and found willets nearly everywhere, walking across the road and among the short grasses of the road berms. In stating this belief that the courting-grounds are separate from the nesting territory, I have considered those cases where the courting-grounds are close to the nesting territory, as well as the fact that high spring tides will often drive the birds onto the territory for an hour or so. I have covered the marshes at all stages of tide and at all times of day to discount any daily or tidal rhythm in the birds' activities.

Nesting

About six days are required for the laying of the four eggs of the normal clutch, and the incubation period is 23 to 24 days (Tomkins, 1932), although Sprunt and Chamberlain (1949:232) state that the incubation in the Eastern Willet takes from 21 to 23 days. My own determination of 23 to 24 days was based on marked eggs in a number of nests, and a review of the data in my notebooks confirms that conclusion.

When Gilbert Rossignol collected a set of eggs, he listed them in his egg

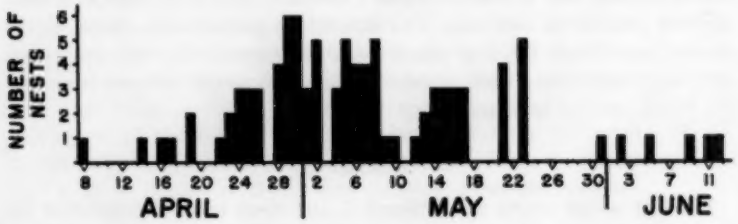

Fig. 1. Seasonal distribution of Eastern Willet clutches, corrected to the beginning of incubation.

record very carefully as "fresh," "slight" or "advanced," referring to the stage of incubation. His egg records from 1907 to 1937 were tabulated as of the date incubation began, and I have added to those the sets covered in my notes which could be corrected to date when incubation started with reasonable accuracy. All other egg records were discarded. The data are presented in Figure 1. The idea was to give a better view of the incubation season than the usual scatter-gun method of listing all dates when eggs were found. It represents nearly 50 years of nesting records (Rossignol's and mine) in the same locality.

The Post-hatching Period

After the eggs are hatched, the nest is deserted very soon, often on the same day, and it appears that the nesting territory has no special value as a home for the family. I have watched nests almost to the hatching point, then a day later found the locality deserted.

Wayne (1910:54) tells of a pair of willets carrying their young away from the nest and across the creek, one by one, until the whole brood was moved. Bent quotes several accounts of other species of shore birds carrying young as follows: European Woodcock, *Scolopax rusticola*, (1927:57); American Woodcock, *Philohela minor*, (1927:68); Spotted Sandpiper, *Actitis macularia*, (1929:90), and there are other accounts of such behavior scattered through the literature. Certainly this behavior might have survival value in marshes subject to tidal overflow, and it may account for the disappearance of the brood from the nesting territory.

The adults are active over the wetter portions of the salt marsh shortly after the eggs are hatched, and show little interest in the nesting territory. It is very difficult to find the young ones then, as the marsh grasses are high enough at that season to provide effective cover. It is also hard to separate the activities of family groups from then on, as one shrieking willet attracts others from far and near, but if one watches from a distance it appears that there is a loose gathering into groups of several families very soon after hatching. Probably as the sexual activity wanes, there is a return of the normal gregariousness characteristic of the greater part of the year, which has to some degree been held in abeyance by the territorial behavior.

On June 29, 1953, Herbert L. Stoddard collected a male willet here that was going through the usual noisy defense of the young presumably hidden in the marsh. This bird had testes about the size one would expect in a winter bird. We thought then that the gonadal regression of the post-breeding season was proceeding rapidly. Both parents share in the incubation duties and both appear to assist in the defense of the young.

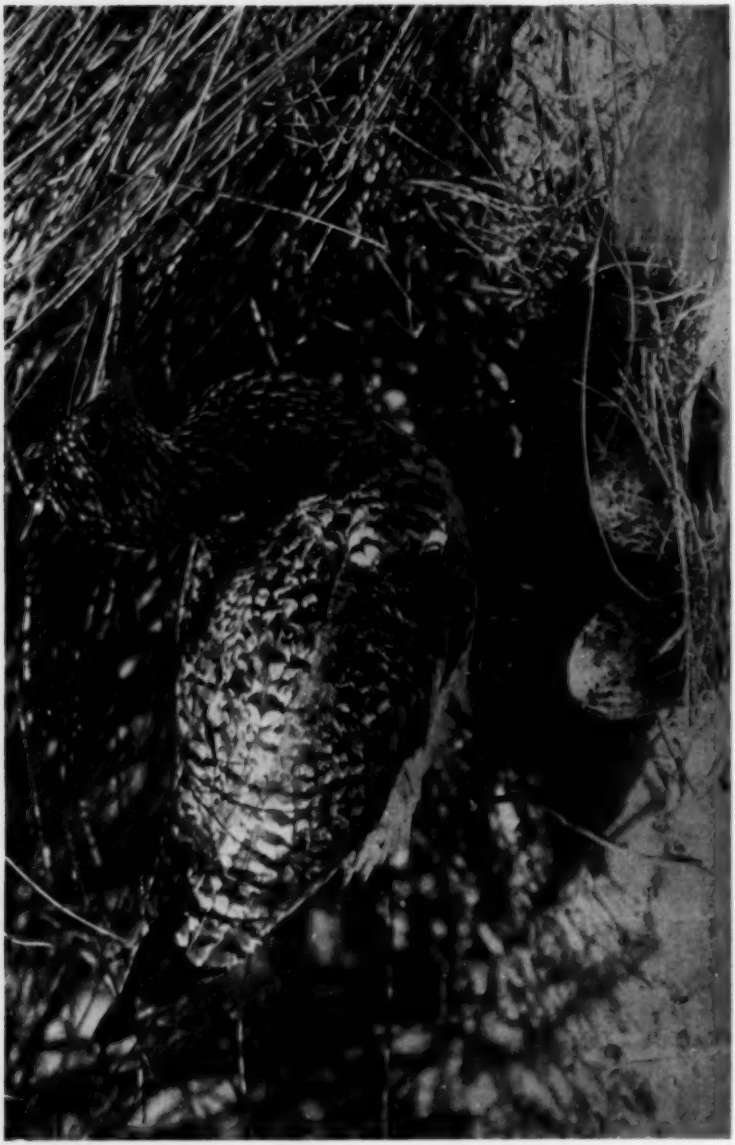

FIG. 2. Incubating Eastern Willet, photographed at Oysterbed Island, Georgia, by Frank N. Irving. Note wear of dorsal plumage.

Fall Migration and Molt

Most of the willets simply disappear from the Georgia coast during late June and July. In an earlier account (Tomkins, 1932), I stated that young and old gather on the beaches for a time prior to southward migration. That statement I now believe to be in error. The flocking which some species exhibit prior to their departure is not conspicuous in this willet population.

There is no time in the brief summer stay of *C. s. semipalmatus* for any extensive molt, either prenuptial or postnuptial. This statement appears to be in contradiction to that of Bent (1929:32) who wrote: "Adults have a nearly complete prenuptial molt in March, April, and May, involving everything but the flight feathers of the wings, which are apparently molted later in the fall or early in the winter. I have not actually seen these feathers molting." Bent was writing of the race in its entirety, and I do not know what the molting birds that he mentions were. Our birds arrive in worn plumage, and continue so during their stay here. The Charleston Museum has no specimen showing what *C. s. semipalmatus* looks like in fresh plumage. Perhaps sometime I shall find a delayed migrant here after the postnuptial molt. The plumage of our breeding birds is well illustrated by the photograph (Fig. 2) which was made by Frank N. Irving over thirty years ago, on Oysterbed Island, Georgia. I am grateful to Mr. Irving for permitting its inclusion here.

The Western Willet

It is desirable to discuss briefly the position of *C. s. inornatus* in this locality. There is a fall migration of this race along the sandbars and outer beaches in late August and September, but the spring migration in February is not so marked, and may easily be missed. Some specimens taken on February 22, 1954, from a flock asleep on the beach in the forenoon had empty stomachs, and were most certainly migrants. A few individuals may be seen at any time of year. Some places will have a few summering birds, or some that stay all winter. The Western Willet occupies a more restricted niche than the Eastern, for it does not frequent the muddy creek banks as commonly, preferring beaches and oysterbeds. The stomach of one specimen of *inornatus* contained many small bivalves and some shrimps of the genus *Palaemonetes,* while three specimens of *C. s. semipalmatus* contained only the remnants of small crabs of the genera *Uca* and *Sesarma.* In summer the foraging range of *semipalmatus* reaches into that preferred by *inornatus,* and it is not unusual to find a shrieking pair of Eastern Willets walking among small groups of the Western form.

Field identification of the two forms is possible with a high degree of accuracy. The Western Willet is fully a head taller and is a gray bird lacking

the heavy streaking of *semipalmatus*. The grayer bird stands out in flight in a good light. When specimens are in hand, it is clear that the lightly-barred breast feathers of *inornatus* could never wear into the heavily speckled ones of *semipalmatus* as we see it here.

Summary

The Eastern Willet (*Catoptrophorus s. semipalmatus*) spends about three months on the coast of Georgia and South Carolina in spring and early summer. This time is divided about equally among courtship, nesting and care of the young. Courtship takes place on exposed reefs in salt marshes and on tidal mud flats, whereas the nesting territories are located in grassy upland areas. I have found no evidence that molting occurs during the willet's summer stay on this coast.

The Western Willet, (*C. s. inornatus*) passes through in fall and in late winter, and a few remain at other times of the year. This subspecies occupies a more restricted niche than the Eastern Willet, and may be distinguished readily from it in the field.

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1231 East 50th Street, Savannah, Georgia, November 7, 1954

THE AUXILIARY BARREL

BY LOYE MILLER

THERE has been much shifting of emphasis in the study of Vertebrate Zoology since I embarked upon it (even though crudely) more than sixty years ago. Still, the collecting of specimens in the field is not an obsolete procedure by any means.

Scarcely a week passes that I do not have inquiry from some graduate student regarding equipment for shooting birds, reptiles or small mammals. Their problem is still a real one. Expert machinists are expensive to employ and they lack familiarity with the problem; hence the present day "do it yourself" slogan might well be brought into play. Adult education classes in night schools at many localities offer facilities and training in the use of power tools. I "learned by doing" forty years ago. Why not try it? These suggestions are offered, therefore, to the novice.

My earliest efforts to avoid the "half-load" for standard-bore shot guns were directed toward the shot pistol (Miller, 1893;1915), a device that still has a very definite function (Schmidt, 1951). Quite a number of shot pistols have been put into circulation for my colleagues and students. They are of great importance to the herpetologist and to the man who "travels light." The auxiliary barrel, however, is the most serviceable device for the serious collector who is working in country with a diversified fauna. A fairly large bore double-barreled shotgun with a .38 caliber (or .410 gauge) and a .22 caliber auxiliary barrel make up a good general armament. Even a few shells loaded with a solid slug to represent the opposite "end of the spectrum" may properly be added to the list.

My first "aux", acquired in 1894, was made by taking one of the brass shells of my 16 gauge gun, boring out the anvil at the base, thrusting in a 10 in. length of brass tubing with an inside diameter of .375 in. and then pouring melted lead into the shell around it. The device was pretty crude and tended to "shoot loose" after a while but it survived many thousands of rounds of firing and was used fully four times to the large barrel's once.

My next effort at improvement (with accent on the effort) was to drill lengthwise through 10 inches of Ford axle with a long-shanked 3/8-in. drill, then remove excess metal beyond the chamber. Automobile axles nowadays are made of "sterner stuff" so commercial *cold roll* steel or even "Duralumin" is employed for our purpose though duralumin is a bit "tricky" to bore after the first inch of penetration. The total length also has been reduced to less than 6 inches for .38 auxes in 16 bore guns. Duralumin and brass have been abandoned because they bruise too easily if dropped.

Ejectors were fitted into the first dozen or so of the .38 and .410 auxes

which I made but the practice was abandoned after proper methods of chambering were developed. The exploded shell is easily plucked out with the thumb and middle finger nails if the chamber is right and is free from fouling.

This museum has standardized its equipment as 16 bore guns with .38 and .22 caliber auxes. At the present moment we are able to buy and stock "Shelby Seamless Steel Tubing" in proper diameters and bore so that it will ream and polish to .38 and .22 calibers. The proper length tube is then "sweated" into a steel block of proper size for the gun chamber. In the final reaming of .38 or .410 pistol barrels the reamer used has the ultimate 1/4 inch of the point tapered by 10 one-thousandths of an inch. This permits leaving a choke of .005 to .010 inches in the bore, a matter of great importance in the shot pistol.

The initial boring. Boring for a center fire cartridge is a relatively simple procedure. The stock selected must be of diameter sufficient to allow for the maximum diameter of rim at the breech. Cut off the desired length of stock rod, true up the ends, center each end with precision and clamp the work in a lathe dog. Select a twist drill at least 1/32 in. smaller than the desired bore. (Better still, select two drills 1/16 in. and 1/32 in. smaller than the bore and bore twice). The standard twist drill can easily be extended by drilling and tapping the shank and screwing in the desired length of drill rod of proper size.

Place the drill in the lathe chuck, bring the work against the drill point, bring the tail stock center up against the opposite end and tighten slightly. Rest the tail of the lathe-dog against the tool carriage and start the lathe slowly, keeping up gentle pressure by feeding in the tail stock screw. After the drill has gotten properly started the lathe speed may be stepped up, but in a long boring there is a tendency to heat up and the drill binds in the hole. A little patience is a good investment. Use plenty of cutting oil. Withdraw and remove chips frequently especially during the first cut. If your drill is properly ground, with the two lips of equal length and angle, it will follow through straight to the tail stock center. (Don't run too far and cut off the tip of that center). A poorly ground drill results in much grief and a discarded piece of work. Repeat with the second drill and follow with a six-fluted reamer tapered at the tip as suggested above and you will have a fairly smooth bore. A piece of 1/4-in. birch dowel, spiral-wrapped with a strip of crocus cloth, will give the final polish.

Boring for the .22 caliber introduces a new factor. A rim-fire cartridge must be struck by a center-fire firing pin. Theoretically the bore should be off center by 1/2 the diameter of the cartridge—i.e. .125 in. (This offset however could not be used in making a .22 aux for a .410 shotgun.) By trial and error I learned that an offset of .080 in. failed to fire, one .090 inches generally fired but one .100 inches was certain if the firing pin were exactly centered (Fig. 1). Too great an offset brings the pin too

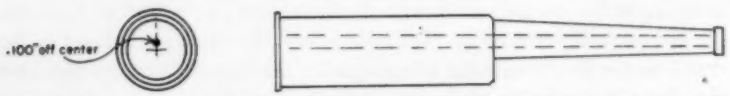

FIG. 1. Ground plan for .22 caliber auxiliary barrel for 16 gauge shotgun. Drawing by Lois C. Stone.

abruptly against the steel block, and one gun with which I had experience tore off the rim of the aux because of its too-powerful hammer springs. The rim gradually yielded with the repeated shocks.

In drilling for a .22 aux the procedure is much the same as for the .38 caliber, except that the offset must be accurately determined and must be on the same radius at each end of the work. This is accomplished readily by using the cross feed screw of the tool carriage which is graduated in thousandths of an inch. Bring a sharp-pointed cutting tool to the exact center, then retract exactly .100 inches and cut a very slight groove. Any point on this circle will have the proper offset. Drag the point lightly across the end and then along the side of the work. Reverse the work in the chuck, continue the fine scratch along the side, then across the face and to the exact center. Retract the cross feed exactly .100 in. and cut a shallow circle: Where the radius scratch intersects this circle determines your point. You then have points on opposite ends of the work that represent the ends of the drilling axis which is parallel to the center axis and .100 in. from it. Place one of these points against the drill and the other against the tail stock center, then proceed with drilling as described above.

In drilling for a .22 aux for .410 gun, a little "fudging" is done in order to leave more supporting metal where the aux tube extends beyond the .410 chamber. The muzzle center is not offset. Theoretically this is all wrong, but practically we find just as good patterns resulting, probably for the following reason: after the charge leaves the aux muzzle the gases confined within the gun bore "shepherd the shot" all the way to the gun muzzle. A little eccentricity at the breech seems to be of minor importance.

Removing excess metal.—Replace the chuck with a face plate and active center. With a lathe-dog the work can then be made to rotate on the axis of its bore between the active center and the tail stock center and against the cutting point. The barrel of the aux, beyond the block, can thus be reduced to the desired thickness and taper. It is wise to leave a slight collar at the muzzle of the aux for the following reasons: (1) it reduces danger of denting the muzzle; (2) it sets up vortex currents in the gas that might otherwise be carried back to the gun chamber. Any deposit of unburned carbon would then tend to form near the muzzle of the aux, thus reducing any tendency to fouling that might cause the aux to stick in the gun chamber.

Chambering the aux. Herein lies the potential source of greatest grief—the stuck shell that has to be rammed out with a stick. The chamber must be extremely smooth and should fit the shell snugly enough so that the brass shell cannot expand beyond the limit of its elasticity and yet will slip out when heated by the discharge.

For the .22 chamber I finally obtained and modified a special chambering reamer for .22 "Long rifle" barrels. This is a six-fluted reamer with a 7/32-in. pilot. The proximal shoulder was cut back sufficiently to allow penetration of the cutting flutes farther into the bore and accommodate the full length of the discharged shot shell. Since modifying the reamer we have had no trouble.

TABLE 1

DRILL AND REAMER SIZES FOR MAKING AUXILIARY BARRELS

Caliber	1st drill	2nd drill	Bore reamer	Chamber reamer
.22	3/16 = .1875 in.	13/64 = .203 in.	7/32 = .2187 in.	Special .227, piloted
.38	21/64 = .328	11/32 = .3475	3/8 = .375	3/8 expansion reamer
.410	3/8 = .375	25/64 = .390	13/32 = .406	13/32 expansion reamer

At this museum we use brass .38 shells retrieved, in part, from the pistol ranges of the police department. Shells are reloaded indefinitely and are "sized" before each reload. A 3/8-in. expanding reamer is used in chambering the auxes. By repeated cut and trial a very nice fit can be accomplished.

In .410 chambers we use stock paper shells. These give less trouble and I have gotten by with a 15/32-in. six-fluted reamer, though a little juggling may be called for on account of the variable brass base of the shells. A 15/32-in. expanding reamer will do this trick—if you have one.

Countersinking the chamber.—The cartridge must be countersunk into the aux a distance equal to the thickness of its rim in order that the breech may be closed.

If you install an ejector, this recessing is best done with a piloted counter bore of proper size (if you have one). The simpler procedure as finally adopted here is as follows: grip the aux in the chuck nearly up to the rim. By using a round-nosed cutting point held at right angles to the aux breech and carefully manipulating the cross and the longitudinal feeds, you can make a shallow open basin in the breech surface that will fully seat the cartridge and also allow room for the finger and thumb nails to pluck out the exploded shell.

If your chambering has been properly done and the aux accurately fitted to your gun you will have a serviceable item of equipment that, if protected from fouling, should give carefree service—until you lose it.

The values given in tables 1 and 2 may be of assistance.

TABLE 2

APPROXIMATE CHAMBER SIZES IN SHOTGUNS

Gauge	Rim diameter	Tapers from —	to
12 ga.	.900 in.	.804 in.	.800 in.
16 ga.	.810	.740	.730
20 ga.	.750	.694	.687
.410 ga.	.530	.474	.468

THE SHOT PISTOL

The shot pistol presents a dual problem. Making a smooth-bore barrel involves no great modification of parts of the above discussion. The main problem is to obtain a lock and stock that is rim fire for .22 or center fire for .38 and which has a cylinder long enough to accommodate the desired cartridge.

If you are in a position to purchase a new gun, follow your own taste. Iver-Johnson Company makes a .22 caliber target revolver with six-inch barrel that is designed for standard "Long-rifle" ammunition. By ordering from the factory they will provide at the same price, the barrel before the rifling grooves are cut. For short range collecting this needs no modification.

If the barrel is unscrewed and replaced with a nine-inch barrel, the range is greatly extended. A 9-inch choke bore for .38 caliber or 12-inch for .410 gauge will make an excellent collecting pistol. If the barrel will not unscrew,

cut it off to a stub, drill it out with a drill smaller than the outside diameter of the new barrel, turn down the outside of the new barrel to the proper size and distance so that it slips into the stub and stops against a square shoulder. This reduced part of the shot barrel is then sweated into the stub snug up to the shoulder. If your machining has been done accurately, the junction is scarcely discernible.

A great variety of pistols, old and new, have thus been converted to peaceful function for the ornithologist or the herpetologist.

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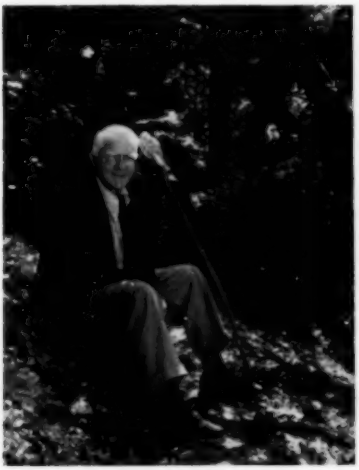
Museum of Vertebrate Zoology, Berkeley, California, May 18, 1955

NEW LIFE MEMBER



Loye Miller, Professor of Biology, Emeritus, at the University of California at Los Angeles, is noted for his contributions to three areas of activity, vertebrate natural history, avian paleontology, and the teaching of biology. A legion of his former students refer to him affectionately as "Padre." Professor Miller, a Fellow of the American Ornithologists' Union, took his Ph.D. in paleontology at the University of California in 1912. Since that time he has investigated a variety of topics ranging from natural history of pelagic birds to territoriality in owls. A rich chronicle of his experiences as a naturalist is recorded in his book "Lifelong Boyhood," published in 1951. For the past several years, Professor Miller has lived in the home of his son, Alden H. Miller, in Berkeley and has maintained an office in the Museum of Vertebrate Zoology.

GENERAL NOTES

Distributional and breeding records of some birds from Coahuila—Summer field parties from the Museum of Natural History at the University of Kansas have collected in the past six years several hundred birds from the Mexican state of Coahuila. Several specimens from this collection warrant special consideration and are discussed below.

Recurvirostra americana. American Avocet. A small breeding colony (8 pairs) of this species was discovered by Robert W. Dickerman on May 19, 1954, 8 miles east and 2 miles south of Americanos, on a large grassy playa traversed by rows of creosote (*Larrea tridentata*). A male (KU 31433) and a female (KU 31432) were obtained. The latter was taken from a nest containing four partly-incubated eggs. Four eggs in a second nest contained well-developed, downy young. Breeding Avocets were previously reported in Mexico only from the state of San Luis Potosí (Friedmann, Griscom and Moore, 1950. *Pacific Coast Avif.* 29:101).

Otus scops flammeolus. Flammulated Screech Owl. Two specimens of this comparatively rare owl were collected by R. W. Dickerman: male (KU 31600), weight 50 gms., testes 8 mm. long, on April 4, 1954, 20 miles south of Ocampo, elevation 6000 feet, pine-oak association; male (KU 31581), testes 10 mm. long, on April 9, 1954, 13 miles east of San Antonio de las Alazanos, elevation 9345 feet, pine-spruce-aspen association. Each specimen has a suffusion of cinnamomeous pigmentation, but represents the grayish phase, as described by Ridgway (1914. *U. S. Nat. Mus. Bull.* 50:729). To my knowledge, these specimens constitute the first records of this owl in the state.

Chordeiles minor howelli. Booming Nighthawk. R. W. Dickerman secured a male (KU 31443) on May 16, 1954, 3 miles north and 4 miles east of San Francisco, elevation 4850 feet. This migrant seemingly represents the first record of the subspecies in Coahuila. Nighthawks were heard and seen frequently in this area, and seven birds were observed in flight simultaneously.

Certhia familiaris americana. Brown Creeper. Van Tyne and Sutton (1937. *Misc. Publ. Mus. Zool., Univ. Mich.*, 37:67) recorded a wintering bird of this subspecies as far southwest as Hot Springs, Brewster County, Texas. Data from two specimens collected by R. W. Dickerman are as follows: female (KU 31612), taken on November 27, 1953, at the base of the Don Martin Dam; female (KU 31587), taken on April 5, 1954, 20 miles south of Ocampo. The latter was originally identified by A. R. Phillips. These specimens constitute the southernmost records for the subspecies. I find no previous records in the literature of the Eastern Brown Creeper in Mexico.

Ridgwayia pinicola. Aztec Thrush. A male (KU 31619), the skull of which was incompletely ossified, was taken on December 15, 1953, by R. W. Dickerman, 5 miles west and 22 miles south of Ocampo, elevation 6000 feet, and seemingly represents the northernmost record for this species, which was previously unknown in Coahuila.

Vireo atricapillus. Black-capped Vireo. Four specimens were taken as follows: 2 males (KU 31493–31494), testes enlarged, May 8, 9, 1954, 16 miles east and 18 miles north of Ocampo (R. W. Dickerman); 2 unsexed specimens (KU 32099–32100), July 3, 1952, Sierra del Pino, 6 miles north and 6 miles west of Acebuches, elevation 5250 feet (Sydney Anderson). These specimens seem to extend the known breeding range of the species south to central Coahuila.

Vireo flavifrons. Yellow-throated Vireo. Bent (1950. *U.S. Nat. Mus. Bull.* 197:288) states, "From the records it appears that within the last generation the yellow-throated vireo has extended its range southward or at least has increased in members in the

southern part of its breeding range." Harrison B. Tordoff collected a male (KU 32103) on June 20, 1952, 2 miles west of Jiménez. This bird was in full breeding condition, and is the first record of the species in Coahuila.

Vireo solitarius cassinii. Solitary Vireo. A male (KU 31589) was obtained by R. W. Dickerman on July 4, 1954, 20 miles south of Ocampo. The subspecies was previously unrecorded in Coahuila.

Molothrus ater ater. Brown-headed Cowbird. One female (KU 31513), was shot by R. W. Dickerman from a flock of eight birds on May 3, 1954, 21 miles south and 11 miles east of Australia. It measured: wing, 102 mm.; tail, 64 mm.; culmen, 17 mm.; tarsus, 26 mm.; ovary 8×4 mm. I find no previous records of this subspecies in the state.

Passerina cyanea. Indigo Bunting. A male (KU 31544) was collected by R. W. Dickerman on May 5, 1954, in San Marcos. This bird (testes 5×4 mm., moderately fat, in worn plumage) was observed chasing another male, and the pursuer in turn, was followed by a female. The territorial behavior (observed for 2 hours) of this bird suggests the possibility of breeding, but no nest was found. This specimen seems to provide the first record of the species in the state.

Aimophila cassinii. Cassin Sparrow. A male (KU 32158) in breeding condition (testes 7×5 mm.) was obtained by Sydney Anderson, 18 miles south and 14 miles east of Tanque Alvarez, on July 6, 1952. Another male (KU 32157), having testes that measured 5×3 mm., was taken by H. B. Tordoff, 9 miles south and 11 miles east of Sabinas, on June 14, 1952. This species was previously unrecorded in the state. —S. G. Van Hoose, *Museum of Natural History, University of Kansas, Lawrence, Kansas, March 12, 1955.*

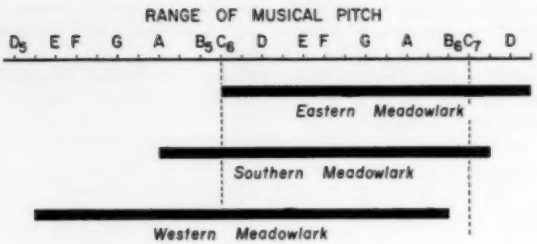
An analysis of the songs of meadowlarks.—In my collection of field records of songs and calls of birds made during the past 40 years, there are 1,050 records of the Eastern Meadowlark (*Sturnella magna magna*). These were obtained largely in Connecticut, but also in several other eastern states. In the years 1950 and 1951 opportunity to travel elsewhere was presented, and I collected 31 records of the songs of the Southern Meadowlark (*S. m. argutula*) in Florida, Georgia, South Carolina, and southern Illinois. I also recorded songs of Western Meadowlarks (*Sturnella neglecta*) on 88 occasions in Oklahoma, Iowa, the Dakotas and Minnesota.

Detailed study of these records leads me to the interesting conclusion that the songs of the southern bird are intermediate between those of the eastern and western birds. This is not particularly apparent in merely listening to the songs, for the qualities of the eastern and southern birds are similar, neither having the gloriously musical voice that the western bird possesses. But details show that the southern bird is closer to the western than is the eastern.

In the matter of time the songs of eastern birds vary from 0.4 to 3.2 seconds in length, averaging 1.55 seconds. The southern bird varies from 0.8 to 1.4 seconds, averaging 1.0 seconds. The western bird varies from 0.6 to 1.8 seconds, averaging 1.2.

The number of notes in songs, counting a slur as two notes, varies from 2 to 9 in the eastern bird, averaging 4.7. The southern bird varies from 3 to 7, averaging 4.6 and the western bird varies from 3 to 11, averaging 6.34.

The pitch of the eastern bird ranges from C_6 to $D\#_7$, a range of 7½ tones. The southern bird is distinctly lower, ranging from A_5 to $C\#_7$, a range of 7 tones. The western bird ranges still lower, from $D\#_5$ to B_6, as shown in the accompanying figure. It is significant that in only 31 records of the southern bird I should find notes 1½ tones lower than the lowest of more than 1,000 records of the eastern bird.



Individual songs of the eastern bird range from 1 to 6 tones in pitch, averaging 2.85 tones. Those of the southern bird range 1½ to 5 tones, averaging 3.17, while those of the western bird range from 2 to 8 tones, averaging 4.3.

In the less exact matter of phonetics, the eastern bird is often entirely clear of phonetic sounds, so far as my ear can determine. Some notes, however, begin with a sound like the letters *ts*, and some link notes together with a sound like the letter *l*. In all of my records only 34 (3.2 per cent) contain the *ts* sound. The *l* sound was found in 112 (10.6 per cent). In the southern bird both *ts* and *l* sounds occur in every song I have recorded. In the western bird *l* sounds occur in every song, and explosive consonants, more like *t* or *k* occur in most of them.

In considering single notes, the eastern bird often sings prolonged notes and slurs, while the southern and western birds sing short, explosive, somewhat staccato notes. However, in the western bird, these are frequently linked together with *l*-like sounds between them.

From these data I would conclude that the Southern Meadowlark is like the Eastern in quality and number of notes, but is intermediate between Eastern and Western in time, pitch and partially in phonetics. It is like the Western Meadowlark in the shortness of notes and the abundant *l*-like consonant sounds. On the basis of certain aspects of the songs, it seems to me that the southern bird is farther removed from the Eastern Meadowlark than its current taxonomic position indicates.

The opportunity to travel and to obtain the data on which this paper is based was afforded by a grant from the American Philosophical Society.—Aretas A. Saunders, *P.O. Box 141, Canaan, Connecticut, March 23, 1955.*

Cattle Egret in Virgin Islands.—On the morning of February 21, 1955, Mr. Anton Teytaud and I visited a pasture at Sprat Hall, St. Croix, Virgin Islands, from which Cattle Egrets had been reported. Immediately upon our arrival at this pasture we sighted 26 white herons. These birds were feeding among a small herd of cattle. An adult Little Blue Heron flew up as we stopped our vehicle. This led us to suspect that these reputed "African Tick Herons" were nothing but immature Little Blue Herons (*Florida caerulea*).

A quick-stalking, heavy-jowled heron near us began weaving its neck in a peculiar snake-like fashion. It suddenly grabbed an insect flushed by a browsing cow. This was no Little Blue Heron. A careful look through binoculars convinced us that these birds were actually Buff-Backed Herons, *Ardeola* (*Bubulcus*) *ibis*. Here before us was not one lone, wind-tossed straggler cast peradventure on this tiny sea-girt island, but a whole flock of 26 rare birds contentedly feeding as at home as could be. None of these egrets was in breeding plumage and only a few exhibited touches of buff on crown, throat and mantle.

After some difficulty a specimen was secured. As the dead bird lay on the pasture the rest of the flock gathered over it in graceful circles.

The bird collected was an immature male. Its measurements were as follows: wing, 234 mm.; tail, 90; tarsus, 87; bill, 56. The iris was yellow, the feet black, and the undersides of the toes yellowish-green, and the tarsus pale yellow. The stomach contents, identified by Dr. George N. Walcott, Agricultural Experiment Station, Rio Piedras, Puerto Rico, were:

	Number	*Per cent of contents*
Schistocerca americana Drury	1	55
Neoconocephalus triops (Linn.)	1	15
Scyllina (*Plectrotettix*) *gregarius* Saussure	7	14
Acheta simmilis (F.)	2	6
Oecantha niveus DeGeer	1	2
Undetermined spiders	3	6
Carabid beetles	3	2

It is to be presumed that these herons came from Puerto Rico, some 90 miles to the northwest of St. Croix. It is estimated that about 100 are presently on the island.—G. A. Seaman, *Box 472, Christiansted, St. Croix, Virgin Islands, March 30, 1955.*

Behavior of migrating birds at sea off San Diego, California.—On April 13, 14, and 15, 1954, the U.S.S. Mount Katmai (AE-16), in which I was serving at the time, was conducting training exercises in a limited area centered 40 miles from San Diego, California, and 15 miles south of San Clemente Island. All three days were overcast, with fog present in varying density at all times. For an hour or so around noon on the 13th four or five Hermit Warblers (*Dendroica occidentalis*) flitted about the ship. Several female Myrtle Warblers (*Dendroica coronata*) were present at the same time. On the next day at about the same hour two Pileolated Warblers (*Wilsonia pusilla*) were seen in company with a small flock of Audubon Warblers (*Dendroica auduboni*) and Myrtle Warblers. Later in the afternoon of the 14th several Mourning Doves (*Zenaidura macroura*), several Audubon Warblers, a Yellow-throat (*Geothlypis trichas*), a Green Heron (*Butorides virescens*), an Ash-throated Flycatcher (*Myiarchus cinerascens*), and an unidentified wren and hummingbird were noted around the ship. On the 15th of April—again around noon—four White-crowned Sparrows (*Zonotrichia leucophrys*), two Sanderlings (*Crocethia alba*), a Black Turnstone (*Arenaria melanocephala*), and an unidentified "peep" sandpiper were seen. At the same time a Rufous Hummingbird (*Selasphorus rufus*) and a Pileolated Warbler were captured by sailors who simply placed their hats over the resting birds.

Opportunities for observation were available at frequent intervals during the three days but neither land nor shore birds were seen at times other than those described. Most of the birds appeared fairly active; the doves, the heron, and most of the warblers would fly out from the ship, sometimes for some distance, and would then circle for a bit before finally returning to alight again on the ship. The turnstone never was seen to land, but for some time coursed low back and forth and roundabout, frequently passing close to the ship's side. The Mount Katmai had one radar set operating at all times, and an additional one in operation most of the time. Other ships in the vicinity presumably always had at least one piece of radar gear in operation also. Whether these electronic emissions causally contributed to the behavior of the birds observed can only be guessed at.—John B. Crowell, Jr., *49 Irving Street, Cambridge 38, Massachusetts, April 30, 1955.*

Hatching of Wood Duck eggs after abandonment.—In the course of studies on the Wood Duck (*Aix sponsa*) at the Patuxent Research Refuge, Laurel, Maryland, I observed an instance of incubation after the eggs apparently had been abandoned by the duck. Several eggs hatched in a nest box during warm summer temperatures, without evident benefit of a setting bird.

On June 15, 1953, a female wood duck was flushed from its nest box containing 15 eggs which were warm and surrounded by a scant amount of down. On June 23 I removed the duck from the nest and fastened over the entrance a protective wooden tunnel of the type designed by the Massachusetts Division of Fisheries and Game to exclude raccoons, *Procyon lotor*, (McLaughlin and Grice, 1952. *Trans. N. Amer. Wildl. Conf.*, 17:242–259).

Five days later, on June 28, the nest box was inspected again but no duck was present. Instead, raccoon hairs were found at the entrance of the tunnel though not on the inside. There appeared to have been no change in the nest since the previous inspection. An "X" was pencilled on the upper surface of each egg so that in a later inspection it would be evident whether the eggs had been turned, as is done periodically by incubating ducks. Before leaving the box, I restored the down to its place over the eggs.

The nest box was inspected again a month later on July 29 at which time nine of the 15 eggs were found still intact and covered with down with the "X" marks still facing upward. The fact that these eggs apparently had not been turned seems to indicate that they had not been incubated by the duck since the time the "X" marks were applied. Ducklings had hatched from three other eggs but were dead in the box, and three more eggs were pipped but the ducklings were dead inside the shells.

The nest box was made of heavy pine boards and erected where it was exposed to the sun during most of the day. Although the insulation provided by the box, together with sawdust and duck down, would tend to "level off" extremes of daily temperatures, the embryos must have been exposed to considerable chilling at night and possibly excessive heating on hot, sunny days. The amount of chilling or overheating that duck embryos will tolerate at various stages of incubation appears to have received little study.

Installation of the entrance tunnel during incubation may have been the primary cause of abandonment, but boxes equipped with these tunnels are used commonly by Wood Ducks. The following year (1954) the same nest box, equipped with the same tunnel, was occupied by a Wood Duck which brought off a brood of ducklings.—CLARK G. WEBSTER, *U.S. Fish and Wildlife Service, Laurel, Maryland, May 1, 1955.*

EDITORIAL

In the course of the preparation of the current volume of *The Wilson Bulletin* several persons have given generously of their time in an advisory capacity. It is a pleasure to acknowledge the substantial aid of George A. Bartholomew, David E. Davis, Thomas R. Howell, S. Charles Kendeigh, Harold Mayfield, Robert Mengel, Van Nolan, Jr., Kenneth C. Parkes, George W. Salt, George M. Sutton, Harrison B. Tordoff, and Josselyn Van Tyne.

WILSON ORNITHOLOGICAL SOCIETY ANNOUNCEMENTS

President Monroe has appointed the following committee chairmen to serve during the year, 1955-56: *Research Grant*, Kenneth C. Parkes; *Membership*, John M. Jubon; *Library*, H. Lewis Batts, Jr.; *Conservation*, Robert A. Pierce; *Endowment*, Robert T. Gammell.

1956 ANNUAL MEETING

Dr. Fred T. Hall, Director of the Buffalo Museum of Science, heads the Local Committee on Arrangements for the Thirty-seventh Annual Meeting, to be held at Buffalo, New York, from Thursday, April 26 through Sunday, April 29, 1956. An innovation planned for this year is a Thursday afternoon field trip to Niagara Falls for early arrivals. The Executive Council will meet Thursday evening. Friday and Saturday sessions will be for the presentation of papers. The Annual Dinner will be held Saturday evening, and there will be a field trip on Sunday. An information circular and call for papers will go out to the membership about March 1.

THE S. MORRIS PELL BIRD ART AWARD

An anonymous friend of the Wilson Ornithological Society has donated a small fund in memory of the late S. Morris Pell, a talented bird artist. From this fund grants of $25 each may be awarded to deserving young bird artists, to be applied toward such purposes as the purchase of art materials or the financing of sketching trips. Applicants should send samples of their work together with a brief statement of background and training (both in art and in ornithology), and financial need, to Dr. Kenneth C. Parkes, chairman of the Research Grant Committee, Carnegie Museum, Pittsburgh 13, Pennsylvania. There is no deadline for applications, and more than one award may be made in a given year.

LOUIS AGASSIZ FUERTES RESEARCH GRANT

In the March, 1947, issue of *The Wilson Bulletin* there appeared an announcement to the effect that an anonymous gift had been presented to the Wilson Ornithological Club with the purpose of inaugurating a series of annual research grants honoring the memory of the distinguished artist-naturalist Louis Agassiz Fuertes. From 1948 through 1955 (except 1953, when funds were not available), yearly awards of $100 have been

made by the Club through a special Research Grant Committee appointed by the President for this purpose. The current Committee feels that the time has come for a review of the Fuertes Grant, listing the previous winners of the award and summarizing the criteria by which applications are judged.

Previous winners of the Fuertes Grant, with the subjects of their investigations, are as follows:

1948 Leonard R. Mewaldt, Montana State University. Life history of Clark's Nutcracker.

1949 Stephen W. Eaton, Cornell University. A comparative study of the genus *Seiurus*.

1950 (split award) Henry E. Childs, Jr., University of California. Population dynamics and life history of the Brown Towhee. Arnold J. Petersen, University of Wisconsin. Reproductive cycle in the Bank Swallow.

1951 Howard L. Cogswell, University of California. Territory size and its relation to vegetation structure and density among birds of chaparral.

1952 Robert W. Nero, University of Wisconsin. Territorial and social behavior of the Red-winged Blackbird.

1953 No award given.

1954 William C. Dilger, Cornell University. Isolating mechanisms and relationships of the thrush genus *Hylocichla*.

1955 Robert G. Wolk, Cornell University. Analysis of reproductive behavior in the Black Skimmer.

It will be noticed that all of the successful applicants to date have been carrying on their ornithological research as university students. *The Committee wishes to emphasize that such an institutional affiliation is by no means required of an applicant.* We wish, in fact, to encourage more applications from non-student amateur ornithologists who may be in a position to make an important contribution to our science.

The most important factor in the judging of applications is the potential contribution to ornithological knowledge inherent in the project submitted. Demonstrated financial need will also be taken into account. Problems in any aspect of ornithology will be considered, except that applications are discouraged for projects which are primarily concerned with wildlife management rather than with ornithology *per se*. It is felt that ample financial support from other sources is available for management projects.

In general, the most favored applicants are those whose researches are already under way. It is fairer both to the Society and to the applicants to award the $100 to a person who has demonstrated that his project is practicable, and who will have a better idea of how to apply his funds than will one whose work is merely in the planning stage.

The Wilson Ornithological Society requests that at least a portion of the results of Society-sponsored research be submitted to the editor of *The Wilson Bulletin* for possible publication, unless prior commitments interfere.

Application forms for the 1956 Fuertes Grant may be obtained from the Chairman of the Committee. Deadline for applications will be April 1, 1956. The Committee's decision will be announced at the annual meeting at Buffalo on April 26, and published in the June issue of *The Wilson Bulletin*.

RESEARCH GRANT COMMITTEE FOR 1956

Kenneth C. Parkes, *Chairman*, Carnegie Museum, Pittsburgh 13, Pa.

John Davis, Hastings Natural History Reservation, Carmel Valley, Calif.

Eugene Eisenmann, Linnaean Society of New York, New York, N.Y.

ORNITHOLOGICAL NEWS

The American Ornithologists' Union held its Seventy-third stated meeting at the Boston Museum of Science on October 25-30, 1955. The first day was devoted to business meetings, the next three days to papers sessions, and the last two days to field trips. The entire slate of present officers was re-elected for one year:

President: Alden H. Miller, University of California
First Vice President: Ludlow Griscom, Harvard University
Second Vice President: Ernst Mayr, Harvard University
Editor of the Auk: Robert W. Storer, University of Michigan
Secretary: Harold F. Mayfield, Toledo, Ohio
Treasurer: Charles G. Sibley, Cornell University

The Brewster Medal was awarded to William H. Phelps, Sr., Caracas, Venezuela, for his fundamental contributions to the systematics of American birds, particularly those of Venezuela.

THE WILSON ORNITHOLOGICAL SOCIETY LIBRARY

The following gifts have recently been received. From:

Andrew J. Berger—3 magazines
L. B. Chapman—1 reprint
H. Everest Clements—1 book
Powell Cottrille—1 reprint
Karl Haller—17 books
Philip S. Humphrey—1 book
Leon Kelso—1 reprint
Margaret M. Nice—2 magazines, 28 reprints
Göran Nordström—1 reprint
Fred M. Packard—27 magazines, 6 reprints
William H. Partridge—1 reprint
William H. Phelps—2 reprints
Miles D. Pirnie—1 reprint
Robert W. Storer—2 reprints, 2 magazines

LETTER TO THE EDITOR

In the March, 1955, *Wilson Bulletin*, pp. 49 and 54, Henry and Virginia Fitch state that the incubation period of the eggs in a nest of the Summer Tanager (*Piranga rubra*) watched by them was eleven days. They knew the dates of the laying of the four eggs, May 29 to June 1, and of the hatching of two of them on the morning of June 12. They found another nestling hatched the morning of June 13. One egg never hatched.

When eggs are not marked and one of them does not hatch it is impossible to be sure of the length of incubation, i.e., the time between the laying of the last egg to its hatching. The authors assumed that the third nestling "probably hatched later" on June 12 and *on this assumption* state that: "Incubation lasted eleven days." It is clear that this conclusion is unwarranted.

MARGARET M. NICE

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WATERFOWL CONSERVATION IN THE DECADE FOLLOWING WORLD WAR II

(A Contribution from the Wilson Ornithological Society Conservation Committee)

During the decade following World War II, the pressures growing out of an increasing human population have added progressively to the difficulty of and need for waterfowl conservation. Moreover, the events taking place during these 10 years have contributed little to suggest that the waterfowl conservationist's road will be any less difficult in the future.

Waterfowl conservation during this period may be reviewed from three points of view: (1) administration, (2) management, and (3) research. As herein considered, administration embraces the political philosophy and financing of waterfowl management; management includes the manipulation of waterfowl populations and habitat; and research concerns the gathering of facts upon which to base the management program.

Administration: The formation of state conservation agencies into councils for each of the four North American flyways has been a significant development in waterfowl conservation. Each flyway council provides a means of formulating regulations tailored, within limits, to the needs of the individual flyway, and, to a lesser extent, to the needs of each state in the flyway.

As an adjunct to each council, the waterfowl biologists within each flyway may serve as a technical group which is available for consultation by the council. This technical group may also act as an agency through which the research activities of the flyway can be coordinated.

The flyway council system creates one potential danger to waterfowl conservation: It may tend to form a pressure group seeking unwarranted changes in hunting regulations. Members of the councils must endeavor to insure that the welfare of the waterfowl remains of primary concern.

Under new leadership, the U.S. Fish and Wildlife Service appears to be following a liberal attitude toward restrictions on waterfowl hunting. When the continental waterfowl population declined in 1953 and 1954, the Service not only adhered to the 1952 regulations on length of season and bag limit for the Mississippi Flyway, but, in 1953, increased the length of season 5 days for the Atlantic and Pacific flyways and, in 1954, added an additional 5 days on the Pacific Flyway. At the same time, the Service permitted California to conduct an experimental feeding program. The result: Hunters in Ohio and Maryland have clamored for similar privileges.

Whether the present liberal policy toward hunting regulations will affect waterfowl populations adversely remains to be seen. In 1953 and 1954 unusually mild weather prevailed over much of the United States during both hunting seasons, thereby tending to limit the kill of waterfowl. With favorable hunting weather, however, an excessive kill of the breeding stock may take place. Within the memory of living men, such unusually severe slaughters have taken place on at least two occasions. The possibilities appear especially dangerous in the Mississippi Flyway where a large portion of the waterfowl which winter there are relatively accessible to the hunter when concentrated. Thus, it seems apparent that the margin of safety guarding our waterfowl population under present administrative policies is paper-thin and that perhaps we are close to being guilty of gambling with the future of our waterfowl resource.

The philosophy of previous administrations of the U.S. Fish and Wildlife Service toward regulating the kill of waterfowl was voiced by Dr. Ira N. Gabrielson, former Director of the Service, in a talk on May 24, 1955, in Washington, D.C. He stated:

"Since the passage of the Migratory Bird Treaty Act, there is no question but what the administrative policy of the Biological Survey and by the U.S. Fish and Wildlife Service has generally given primary consideration for the welfare of the waterfowl resource. Since the welfare of the ducks and geese is the prime consideration, it is necessary to be somewhat *conservative* in making regulations."

Although the Wood Duck population in the Mississippi Flyway has steadily declined in recent years, the Mississippi Flyway Council recommended that the closed season in force in 1954 be changed to permit one in the bag and in possession in 1955. The U.S. Fish and Wildlife Service accepted the Council's recommendation. In view of the precarious status of this species in the Mississippi Flyway, this decision appeared inconsistent with the need for being conservative in making regulations.

The budget of the U.S. Fish and Wildlife Service in recent years has not been adequate. This has resulted in the use of duck stamp funds for purposes other than those intended when the Duck Stamp Act was passed by Congress. The Act was passed at the behest of sportsmen who had become aware of the need for obtaining and developing lands for waterfowl refuges. The funds have had to be used for activities of the Game Management Branch and the operation and maintenance of existing wildlife refuges to such an extent that only minor acreages have been purchased by the Service during the past 5 years. Larger proportions of these funds should be earmarked for the purchase of refuge lands in the future.

Management: One of the most pressing management problems is that of alleviating crop depredations by waterfowl in southern Saskatchewan and Alberta, and in California. Hazing by aircraft, scaring devices, permit shooting, and feeding have been used with some local success, but the affected areas have been so extensive that "only the surface has been scratched" by the control efforts.

The draining of pot-holes in western Minnesota and in North and South Dakota has abated as a result of a change in policy by the U.S. Soil Conservation Service, but this remains as a continuing threat to the most important waterfowl breeding ground in the United States.

Many of the river basin programs planned by the U.S. Corps of Engineers in the southern United States will drain tens of thousands of acres of overflow bottomland used by wintering Mallards and Wood Ducks. Conservationists should familiarize themselves with the recommendations of the Branch of River Basins of the U.S. Fish and Wildlife Service and then urge Congress to include these recommendations before approving any drainage project.

The state conservation agencies are to be commended for their extensive acquisition and development of waterfowl habitat during the past decade. Prior to World War II, only a few states maintained waterfowl refuges and public shooting grounds. Since the war, however, numerous states have acquired such areas for waterfowl. The acreage in state ownership now approaches that held by the U.S. Fish and Wildlife Service. Because of the large amount of waterfowl acreage being lost as a result of drainage, siltation, and industrial and real estate developments, it is hoped that state conservation agencies will continue an aggressive program of land acquisition for waterfowl.

Research: Two notable programs in waterfowl research were initiated by the U.S. Fish and Wildlife Service during the post-war years: (1) the extensive appraisal of waterfowl populations and of production of young on the breeding grounds and (2) large scale banding of adult and young waterfowl on the breeding grounds. These two programs have added valuable information to the knowledge of waterfowl and aided in their management in North America.

Intensive research on nesting waterfowl by members of the Delta Waterfowl Research Station, by Jerome Stoudt of the U.S. Fish and Wildlife Service at Redvers, Saskatchewan, and by biologists of Ducks Unlimited have supplemented the extensive breeding grounds surveys. In our opinion, however, there is a need for additional intensive research on nesting waterfowl.

An inventory of the wetlands of the United States has recently been completed by the Branch of River Basins of the U.S. Fish and Wildlife Service. This is an important contribution toward better land management for waterfowl because it points up the relative value of existing areas for waterfowl, and the areas most in need of acquisition. It is anticipated that the Branch of River Basins will continue to refine its wetland inventory data. It is hoped that eventually the waterfowl carrying capacity of every important water and marsh area will be evaluated.

Studies on two major diseases of waterfowl, botulism and lead poisoning, have produced some new and encouraging findings. Bell, Sciple, and Hubert (1955. *Jour. Wildl. Mgt.*, 19:352-357) have contributed importantly to our knowledge of avian botulism by developing their microenvironment concept and establishing that *Clostridium botulinum* type C grows and produces toxin in immature forms of insect carcasses in distilled water. Evidence from intensive investigations by personnel of the Section of Game Research, Illinois Natural History Survey, has been interpreted to indicate that lead poisoning is less important as a mortality factor among waterfowl than was formerly feared.

During the fall of 1954 waterfowl biologists in every state in the Mississippi Flyway made bi-weekly estimates of waterfowl populations in their state. Upon compilation, the data provided much needed information on the migration of the waterfowl in and through the flyway. Among many values to be gained from this information may be mentioned one—that of providing for open seasons at the most judicious times.

It is believed that further investigations on the precise nature of crop depredations by waterfowl and techniques for the control of such depredations are also among the foremost research needs.—Frank C. Bellrose and Thomas G. Scott

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NEW LIFE MEMBER

Mrs. John William Conboy (Esther Cogswell) received her A.B. Degree from Franklin College and did graduate work at Indiana University and the University of Illinois. She teaches Biological Science in the public schools in South Bend, Indiana, and shares field birding and the making of nature movies as hobbies with her husband. She is also a Life Member of The American Ornithologists' Union.

ORNITHOLOGICAL LITERATURE

AN INTRODUCTION TO ORNITHOLOGY. By George J. Wallace. New York; The Macmillan Company, 1955: 6¼×9¼ in., xii+443 pp., 180 figs. $6.00.

This book aims to fill the need for an introductory text in ornithology dealing with the whole field in a nontechnical yet academic manner. It is to be recommended for use in courses for college freshmen and sophomores or in courses of cultural aim for the layman.

The book starts with the historical background of man's interest in birds together with comments on opportunities today for professional work in ornithology and the extent of amateur activity. In the next four chapters the bird itself is described as a member of the animal kingdom, and its external and internal features are discussed. A chapter is devoted to sense organs and behavior. Three full chapters are given to annual cycle and one to migration. From then on the topics cover a wide sweep, with separate chapters on the distribution of birds, food habits and economic relations, conservation and management, classification and nomenclature, the fossil record, ornithological methods, and even ornithological organizations and their journals. The book is concluded with a bibliography of 314 titles and a 31-page index.

The broad range of subjects which must be included in a modern textbook of ornithology is impressive. In this book the excursions into anatomy, physiology, behavior, classification, practical management, history, and many other topics reveal how involved the science of ornithology has become. Obviously it is now difficult to prepare a textbook giving fair representation to the many facets of ornithology and yet held sufficiently brief and simple for students with slight background in biology. The author has definitely succeeded in touching on almost every active phase of ornithology. The difficulties which become apparent here and there have resulted in part from attempting to keep the book down to beginners' size.

An outstanding merit is the comprehensive coverage of modern research as reported in the American ornithological journals through 1953. A fair number of foreign research reports are also cited. Documentation is quite thorough. Bibliographic entries are conveniently located at chapter endings and in the terminal bibliography and include titles. This is a truly strong feature and will be useful to students seeking to go beyond the often tantalizingly-brief extractions presented in the text itself. In many places the information cited is alluded to so briefly as to make a reasonable understanding of it impossible short of recourse to the original papers. This makes reading for the students laborious and frustrating. The book has an elementary flavor, belying its nature as a compact summary of recent information, due to the inclusion of trite background material on birds, such as is found in many standard zoological texts.

The three especially-valuable chapters on annual cycles are effectively illustrated with many photographs from nature. Elsewhere, however, some of the illustrations, such as photographs of mounted birds, lack interest. It would increase the meaning of the sketch of the soaring hawk, page 119, if the reader were informed as to whether it was drawn from direct observation or from a photograph. The explanation of territoriality is accompanied by a hypothetical map, page 128, whereas a genuine example would be preferable.

Few important research papers have been overlooked, but a valuable addition to the discussion on distribution of birds in relation to life zones, ecologic formations, and biotic provinces would be a reference to A. H. Miller's, "An Analysis of the Distribution of the Birds of California." Little is given on the physiology of annual cycle

mechanisms, though recent ornithological research articles discuss this topic vigorously. The word chromosome does not occur in the index, though the Japanese workers since World War II have reported several pioneer cytological researches significant to avian systematics and evolution.

The chapter on ornithological methods refers to procedures which may be applied by the bird watcher and student of life histories. Yet elsewhere in the book one misses practical information which would instruct the student how to carry out original studies of his own, as, for instance, if he wished to analyze molt in a specimen at hand. Research techniques have not been included to the degree that this book could serve as a handbook or tool. However, the author has pointed out the need for research in many places.

This volume is cast as a beginner's text, and it has been written in such a way as to preserve its usefulness to beginners in the classroom. Undoubtedly it will serve as an effective springboard for participation in ornithological work by students and amateurs. For the more advanced worker it provides a summary of recent work and a convenient guide to modern literature.—PAUL H. BALDWIN.

THE WATERFOWL OF THE WORLD. By Jean Delacour. Vol. I—The Magpie Goose, Whistling Ducks, Swans and Geese, Sheldgeese and Shelducks. Country Life Limited, London, 1954: 8 × 10 in., 284 pp., 33 maps and 27 color plates by Peter Scott. $15.00.

This is the first of three volumes which will provide for the first time a monographic treatment of the waterfowl of the world. It will be hailed as the successor to Phillips' "A Natural History of the Ducks" both because it brings up to date the information and advances in approach of the 30 years since that classic work appeared and because it is much more comprehensive in its scope—it includes the swans, geese and many related and aberrant forms in addition to the true ducks and their relatives. It will be further welcomed because, unlike Phillips, it will be readily available in all libraries and not beyond reach of the individual with a deep interest in this group. Large format, excellent typography and 16 color plates explain the cost.

Both author and illustrator of these volumes have a wide first-hand knowledge of the species through extensive travel and both have lived with most of the species in their aviaries. Thus they have acquired an immense knowledge through day-to-day observations throughout the year. This should provide unusual accuracy in depicting the species in color and in describing their behavior. Any one who pursues this volume will be impressed with the quality of the results.

When an artist must show 12 to 23 birds on a single plate, large enough to depict taxonomic details, he must make illustrations and not paintings. Some may complain that they are too monotonous for illustrations in such a large work and they certainly are reminiscent of the field guide style. However, Peter Scott's skill in arranging so many birds on a plate without making it seem crowded is indeed amazing and shows him to be a master of design. The frontispiece showing Pinkfeet coming in to winter quarters is more in the Scott tradition.

Most of the plates are well executed and the publisher is to be congratulated. However, the color of the bill of the juvenile Black Swan of Plate II is not "brownish black with the nail whitish" as called for in the description.

The present volume is primarily concerned with matters taxonomic, distributional and avicultural. It includes the subfamilies *Anseranatinae* (the Magpie Goose); the *Anserinae*, all true geese, swans and whistling ducks (formerly known as tree ducks); and the

first of the tribes of the *Anatinae*, goose-like ducks, shelducks, South American crested ducks and the steamer ducks.

In the introduction Mr. Delacour quotes from his previous paper with Ernst Mayr (1945. *Wilson Bull.*, 57:3-55): "The new classification of the duck family that we propose attempts to do two things: to arrange the species in related groups and in a natural sequence, and to adjust the nomenclature of species and genera to progressive concepts of these categories." The present volume and those to come are to expound further these newer concepts. The influence of this genetic sophistication in making interpretations of species ranges and relationships is evident throughout the volume. It is to be hoped that, with this more formal presentation, this newer approach will gain wide acceptance and may find its way into the A. O. U. Check-list.

The range maps are very clear and will be a most welcome feature of the volumes. Occasionally it is not clear whether the original or present range is depicted (e. g., that shown for the Magpie Goose must not be recent.)

Areas of overlapping breeding range are sometimes referred to as mixed populations (*Anser anser* subsps., p. 100), implying that intermediates are not found and that some isolating mechanism other than a geographic barrier is in operation. But the text shows clearly that intergradation does occur, just as in Bean Geese, *Anser fabalis*. It is not clear what distinction is intended.

From the recent work of Yamashina and others we are told that swans and ducks have the same chromosome number (84 in males) but that the true geese have 90. It is gratifying to learn that chromosome number is not taken as an infallible criterion of species and their phylogeny, a concept so common among the current crop of plant taxonomists. Instead Delacour says: (p. 91) "The significance of chromosome number in establishing relationships is still obscure, and probably of doubtful value."

The literature cited by the author is drawn from a great variety of sources both historical and modern. It is rare to find a man equally aware of sources in both Old and New World. He quotes freely from the best modern works, such as Austin's "Waterfowl of Japan" and Salomonsen's "The Birds of Greenland" and adds a host of unpublished communications and personal observations. His knowledge of avicultural history and practices is most surely unsurpassed in the world today. For those who are not enthusiastic aviculturists the space devoted to this subject (frequently half the total pages allotted the species) may seem out of balance and often a bit tedious.

One searches in vain for much biological and ecological information. Weight data are seldom given and there is no mention of the cloaca and its associated structures so commonly used in America in analyzing age and sex composition of populations handled in banding operations. In fact there seems to have been little use made of band recovery data from North America or Europe. This may stem in part from the fact that most of the goose banding data in America remains in the Washington files, unpublished.

I believe the balance in use of literature is sometimes open to question. For example, trivial unpublished facts are included in the General Habits of the Lesser Snow Goose (including the Blue Goose as a color phase), but no mention is made of Soper's two outstanding works on the species (1930, "The Blue Goose," *N. W. T. Br. Dep. Int. Canada*, and 1942. *Proc. Boston Soc. Nat. Hist.*, 42:121-225).

But we must not judge too harshly now as to omissions, for we are promised in the Introduction that a general account will be given at the end of volume three. "It will include chapters on morphological, anatomical, and biological characters; on history, sport, conservation, acclimatization, care and breeding, and a bibliography." Let us hope that it will be a large volume!

The usual extravagance of publishers' claims is shown on the dust jacket, which says that these volumes will include "all that is known of the waterfowl of the world." I find that the behavior literature dealing with geese is barely mentioned although several striking original observations are included. One is the fact that aggressive behavior in both swans and geese depends on the similarity of plumage pattern of the intruder and not upon the size. Further (p. 93) the pre-flight intention movement of side-to-side shaking of the head is given as a general characteristic of geese.

A few old wives' tales seem to me to be perpetuated. The notion that Cape Barren Geese will abandon their nests if the eggs are touched by human hand (p. 201) taxes my credulity. Also, if "Flocks migrate in V-shaped formations or trailing lines, *led by an old bird*" (p. 99, italics mine), I should like to know the evidence. This thought has long appealed to my imagination but I have never found support for it.

Again one would like to know the evidence for the following statement made concerning Canada Geese (p. 152). "Various populations have repeatedly changed their breeding grounds, flyways and wintering areas as a result of egg collecting, drives and slaughter by northern natives, and of excessive shooting farther south." I have followed the literature on this species closely for many years and have never found evidence for shifting breeding grounds. Shrinkage, yes, but if much of this shifting went on, the reproductive isolation leading to the extreme subspeciation found in this group would not have occurred.

It is welcome to find that 11 geese of the confusing Canada group have been treated as one species, with 12 admittedly tentative subspecies recognized. Since morphometric differences and behavior deviations will undoubtedly be found between each population (and the banding evidence indicates that there are dozens of them), it is hoped that all will not have to be given common names as this type of information accrues.

Common names must be somewhat arbitrary and no one would agree with all that are used. But this is the author's privilege since he must draw from both A. O. U. and B. O. U. lists and add many from other faunas. Some will deplore the continuation of common names for subspecies, especially for those that cannot be distinguished in the field. These common names tend to sanctify the subspecies in the mind of the layman who has difficulty in accepting the idea of tentative names. The American public will never accept brent for brant. Again, there is inconsistency in forming common names for species complexes. All the *canadensis* group have Canada inserted in the name—even to the Cackling Canada Goose; but in the *fabalis* group the Pinkfoot does not become the Pink-footed Bean Goose!

I have long been impressed with the fact that the subspecies of Canada geese do not follow Bergmann's rule but are arranged in the opposite manner. In fact, they show a graded series in size from the large southern forms, *fulva*, *moffitti*, *maxima* and *canadensis*, to smaller more northerly *occidentalis*, *taverneri* and *parvipes*, to the smallest forms, *minima* and *hutchinsi*, breeding on the north sea-coasts and islands. This is clearly shown in Plate VIII but the generalization is not found in the text.

It is disturbing to see the emphasis taxonomists have placed upon measurements of soft parts, because Alpheraky pointed out many years ago (1905) that these structures, especially length of bill, differed in size in the two sexes and increased continuously with age. This basic feature of growth in geese seems to have been ignored until the present work.

The use of similar headings in discussing genera, species and subspecies leads to considerable duplication. For instance, there is great similarity in the discussion of General Habits under *Anser*, *Anser anser*, and *Anser anser anser*, and we are told in three

different places that it was the Atlantic Canada Goose that was introduced into New Zealand.

All in all, this volume is a rich compendium of both the old and the new, interestingly presented and well written. It is a volume that every man interested in waterfowl will want to own.—WILLIAM H. ELDER.

THE SPECIES OF MIDDLE AMERICAN BIRDS. By Eugene Eisenmann. Transactions of the Linnaean Society of New York (vol. 7, no 1), New York, 1955: 6×9 in., vi+128 pp. $2.00.

The main purpose of this little book is to provide a suggested list of English or "common" names for the benefit of persons visiting Mexico or any of the Central American countries. However, a number of other useful features are included. It offers a list of technical names and numerous foot-notes pointing out the differences of opinion of taxonomists concerning the matter of those names. The range of each species is given in a general way and there is a short discussion of distribution in the Introduction. An ample, well-selected Bibliography is included.

The names provided are intended to apply to "species," without regard to races. However, it seems that we will never know just what constitutes a species and there is no end of opinions as to just which and how many subspecies should be included in a given species. Thus, the list has to reflect, more or less, the author's views on taxonomy. On this point Eisenmann is very fair in his presentation of the views of other authors and he almost always mentions in the foot-notes the fact that other authors may consider what is listed as a full species as being only a race of some other group or vice versa. All of this points up the futility of an attempt to provide a single vernacular name for a "whole species". Species are "lumped" or "split" so frequently by the taxonomists that the amateur field student should not be expected to change his "common" name for a bird, which he has long known, just because there has been a new technical grouping suggested, and his bird has now perhaps been made a race of some South American species that he never heard of before. From the point of view of a field student, any bird which is easily separated in the field by appearance or song from a species group to which the systematist says it belongs (because of real or supposed evolutionary connections), deserves a separate and distinctive vernacular name.

The English names are not as carefully selected as the technical ones and the list contains far too many new names which either were invented by the author or picked up from one of the other writers who have recently shown a desire to develop new "common" names for birds. While a very few new names, proposed to replace others which had become confused in one way or another, would be welcomed by the field students, a multiplicity of new names is so annoying that all are likely to be ignored. Even the name of a family is changed—the time-honored name of the Dendrocolaptidae, the Woodhewers, is changed to "Woodcreepers". A foot-note suggests that this is done because the word Woodhewer (a translation of the scientific name) is a misnomer. This is indeed a deplorable move, not just because the statement that the name is a misnomer is erroneous (some of these birds do hew wood, and quite vigorously at times) but because the scientific name must remain the same whether it be a misnomer or not, and also because Woodhewer has become so well established in the literature from many decades of use. As a matter of policy it is quite useless for one person to change any name because he thinks it a misnomer. In the first place a name is just a "handle"

and it matters not what it is as long as those who use it know what is meant and are satisfied with it. In the second place any new name invented (no matter what it is) to replace the supposed misnomer will in turn be pronounced a misnomer by some other person.

In criticizing the older names such as those from the "Birds of North and Middle America" by Ridgway, it is stated that some of these names have been used to denote more than one species by different authors as though this were something to be abhorred. However, Eisenmann changes the name of the Allied Woodhewer (*Lepidocolaptes affinis*) to Spot-crowned Woodcreeper, although both Hellmayr in "Catalogue of Birds of the Americas" and Chubb in "The Birds of British Guiana" apply the name Spotted-crowned Woodhewer to a bird of a different species. No warning is given even in a foot-note that the name has in the past designated a quite different bird and the reader is not even informed that the name "allied" has been applied to the species in all other literature. When a new name not only attempts to change an old, well-established name about which there never has been any confusion or dispute but actually muddles the name of another species, it is hard to understand what the author is really trying to do. As is illustrated in the example above, another new feature of the vernacular names is that the "doubling of the past participle is avoided for simplicity and euphony." It is doubtful if such a feature really simplifies and some readers might think that "Spot-breasted", for instance, should be applied as a name to a bird with only one spot on its breast rather than to one with many spots.

So called descriptive names are given in place of old patronymics and geographical names as the author says the new, more descriptive names aid in identifying or remembering a species. This might or might not be true. In the case of the Boucard Tinamou, we have a bird which was described as *Tinamus boucardi* in 1859; it has never had the species name changed, although it has been moved into the genus *Crypturellus*. It has been known since the earliest days by the English name taken from the scientific specific name. It has not been called by other common names and there has never been any suggestion of confusion or doubt about what anyone meant when he spoke of Boucard's Tinamou; in addition we had the considerable advantage of having vernacular and technical names that were alike. Still, a new name was given the bird, that of Slaty-breasted Tinamou. Aside from the fact that the new name is longer and a bit awkward, it provides no information that aids in identification of the bird in the field, as this tinamou, when seen in the woods, appears to be the same color all over. Hence the new name merely adds confusion in an area where there had previously been none.

Numerous other examples could be cited where old, established names are replaced by less desirable ones because the old ones were thought to be misnomers, nondescriptive, misleading or were of a subspecific nature. It is surprising to note in regard to the last-mentioned category that in some cases a well-established "subspecific" name that might well serve as a name of the whole species in case the name of the nominate form were almost unknown or otherwise undesirable, was discarded in favor of another subspecific name which was itself almost unknown or less suitable than the one discarded.

Thus it is seen that the list of vernacular names would not serve to acquaint a beginner with the names in use by a majority of field men already working in the area, and that it would prove confusing and an actual hindrance to him if he consulted it to identify some bird he found mentioned by common name in an old book or magazine. Consequently, it is likely that the book will prove useful chiefly in ways other than that of its primary purpose.—L. Irby Davis

THE WILSON BULLETIN

A Quarterly Magazine
of
Ornithology

KEITH L. DIXON
EDITOR

WILLIAM A. LUNK
ILLUSTRATIONS EDITOR

Volume 67
1955

Published
by
THE WILSON ORNITHOLOGICAL CLUB

THE NATURAL REGULATION OF ANIMAL NUMBERS. By David Lack. Oxford University Press, London, 1954: 6×9½ in., viii+343 pp., 52 text figs. $5.60.

For the serious ornithologist this book is required reading. In a series of chapters a wealth of data about birds is clearly presented. Lack starts out by showing that many populations remain nearly stationary in numbers for periods of years. Then he discusses the significance and variations in clutch size and the breeding season which, of course, determine the reproductive rate of birds. Also, he brings together the data about relation of number of eggs to density of population, which in many cases vary inversely. The next phase in the analysis of regulation is the discussion of mortality. Lack devotes 4 chapters to losses of eggs and young, adult mortality, sex differences, and dependence upon density. The viewpoint now changes from a consideration of forces for increase and decrease to a study of the factors in the environment. Food is described as a limiting factor and then predation and disease are considered. A couple of chapters are squeezed in about the factors limiting mammals and fish and insects just before a series of chapters that, to this reviewer, seem to be a collection of discrete topics that lack a theme. There is a discussion of climate and range, of cycles, of irruptions, of migration, of dispersion and of gregarious and territorial birds. The 4-page conclusion summarizes the main points of the general argument.

No review can cover all the items of importance in a book of this type. Certainly a wealth of data is collected and provocatively analyzed. However, the author may at times seem to stress some ideas more than their general merit permits. For example, Lack at once (p. 21) begins his review of the significance of clutch size. Yet a basic assumption (p. 21, line 16) is that birds are indeterminate layers, which seems to be the exception rather than the rule. It would seem desirable to present the facts as now known and then speculate on their significance. Another question arises concerning the frequent claim that clutch size is related to food supply. Data that illustrate the point are meager because it is difficult to get an experimental situation. Even so, how does this come about—through gonadotropins?

In some places the meanings of terms are not clear. For example, on page 91 in the discussion of avian mortality, Lack does not state whether he is referring to death rate (the number dying divided by the average population) or the probability of dying (the number dying divided by the initial population). Clarification of terms is essential in these confusing problems.

The book is splendidly printed and has only a few typographical errors. The bibliography of 42 pages is an excellent source of references to original data. The index is divided into taxonomic groups and also according to author and subject.

A most valuable aspect of this book is the demonstration that data collected by the amateur in his ordinary pursuits are valuable. The records of clutch-size and nesting dates as well as the results of banding are a real contribution to knowledge.—DAVID E. DAVIS.

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This index includes, in addition to names of species and authors, references to the following topics: anatomy, behavior, conservation, embryology, food, fossils, geographic localities, measurements, migration, nesting, physiology, plumages, predation, taxonomy, voice, and weights. Also included are references of biological significance to mammals and reptiles. Names of new forms described in this volume are printed in **boldface** type.

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This issue of *The Wilson Bulletin* was published on January 11, 1956.

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OF THE

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AT

BUFFALO, NEW YORK

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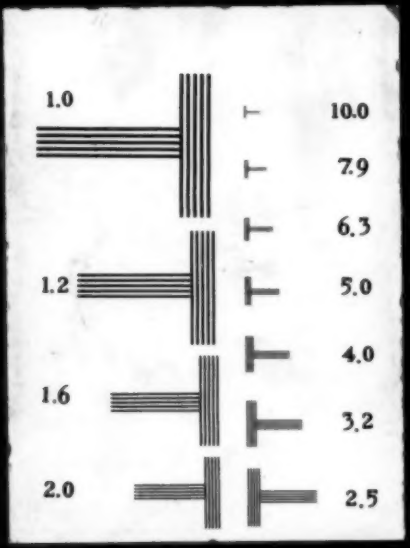

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In microfilming, it is necessary to determine the reduction ratio and multiply the number of lines in the chart by this value to find the number of lines recorded by the film. As an aid in determining the reduction ratio, the line above is 100 millimeters in length. Measuring this line in the film image and dividing the length into 100 gives the reduction ratio. Example: the line is 20 mm. long in the film image, and $100/20 = 5$.

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